JOURNAL OF AGRICULTURAL RESEARCH

VOL. XXI WASHINGTON, D. C. APRIL 1, 1921 NO. 1

OBSERVATIONS ON THE BODY TEMPERATURE OF DRY COWS

By MAX KRISS [1]

Associate in Animal Nutrition, Institute of Animal Nutrition, The Pennsylvania State College

COOPERATIVE INVESTIGATIONS BETWEEN THE INSTITUTE OF ANIMAL NUTRITION OF THE PENNSYLVANIA STATE COLLEGE AND THE BUREAU OF ANIMAL INDUSTRY OF THE UNITED STATES DEPARTMENT OF AGRICULTURE

The normal temperature of the animal body is never a constant figure. It varies in different species, in different individuals, and is never absolutely constant even in the same individual. The observations on the body temperature of man are numerous and more or less conclusive, while relatively little attention seems to have been given to the study of the variations in the body temperature of farm animals under different conditions which are known to affect the temperature of man.[2]

In healthy warm-blooded animals, notably cattle, as well as man, the body temperature fluctuates within very narrow limits. When, however, the normal processes of the body are upset, the temperature may vary widely, and for this reason body temperature is looked upon as an index of health. But aside from this and from any other physiological significance that it might have, knowledge of the normal course of fluctuations in body temperature of cattle has grown in importance with the perfection of the respiration calorimeter used in the investigations on metabolism with cattle.

By means of the respiration calorimeter the heat produced by the animal during a certain period of time, as well as the gaseous exchange between the animal and the atmosphere that surrounds it, is measured. But in order to determine accurately the heat production as distinguished from the heat emission, a knowledge of the storage or loss of heat by the animal body is indispensable. If at the end of an experimental period

[1] I am under obligation to Dr. H. P. Armsby for the opportunity to carry out this investigation, and I wish to thank him for his invaluable suggestions and kindly criticism. I also wish to thank the other members of the staff, especially Prof. J. A. Fries and Prof. W. W. Braman for the interest they have shown and for the suggestions they have given me.

[2] PEMBREY, M. S. ANIMAL HEAT. *In* Schäfer, E. A., ed. Text-Book of Physiology. p. 785–867, fig. 76–82. Edinburgh, London, New York, 1898.

the body temperature of an animal weighing 400 kgm. is 1° C. higher or lower than that at the beginning, it would mean, in the first case, a storage and, in the second case, a loss of heat by the body amounting to 332 calories (assuming the specific heat of the body to be 0.83). Such a quantity would be too large to be entirely ignored in accurate determinations of heat production.

It has been generally claimed that in 24- or 48-hour respiration calorimeter experiments no serious error is introduced by the assumption that the body temperature is approximately the same at approximately the same hour of the day. It was the main purpose of this experiment to obtain data regarding the extent and the course of the body temperature variations in cattle and to study some of the factors that might influence them. With this object in view, observations on the body temperature of cows have been made with reference to the study of the following:

1. Variations in body temperature from about 7.30 a. m. to about 5.30 p. m., including the effect of water drunk.
2. Thermal gradient in the body.
3. Variations in body temperature from about 5 p. m. to about 7 p. m., including the effect of the feed.
4. Effect of the act of defecation and of change in position.
5. Daily variations in temperature measured at exactly the same time of the day.

SUBJECT AND CONDITIONS OF THE EXPERIMENT

It is essential, in order to get comparable results, that the temperature observations on the subject be made under as strictly uniform conditions as practicable. This condition of the experiment fortunately existed to great satisfaction, since the animals used for this experiment were those used at the same time at the Institute of Animal Nutrition for metabolism experiments with the respiration calorimeter, in which strict control of feeding, environment, etc., is maintained. It may perhaps not be superfluous to give a complete description of the animals used for this experiment in order that a fuller appreciation of the individual variations in body temperature may be later had in considering the experimental results.

DESCRIPTION OF THE ANIMALS

The animals used were two dry cows, No. 885 and No. 886. They are both pure-bred registered Jerseys. Cow 885 was born on March 27, 1914, and dropped her first and last calf on September 15, 1917. Cow 886 was born on July 13, 1914, and dropped her first and last calf on October 10 1917. They weigh about 400 kgm. each and resemble each other very much in respect to both size and color.

Both cows were in good health throughout the experiment.

LOCATION

The cows were located during the experiment in the institute barn, which is a closed wooden building provided with a coal stove so that the temperature of the room could be kept fairly uniform.

TIME AND RATIONS

The investigation covers a period of some 16 weeks from December 1, 1919, to March 22, 1920. The cows were kept on a maintenance ration, except that from December 20, 1919, to January 24, 1920, cow 886 received a supermaintenance ration, and from January 10 to February 7, 1920, cow 885 received a supermaintenance ration, about 1.5 times the maintenance ration in both cases.

FEEDING AND WATERING

The cows were fed twice during every 24 hours, at 6 a. m. and at 5 p. m., unless the time was changed for experimental purposes, in which case it has been specified. They were watered only once a day, at about 8 a. m., the amount of water drunk and the temperature of the water being recorded.

BARN TEMPERATURE

A continuous record of the temperature of the barn was obtained by means of the Columbia recording thermometer. But besides this the temperature of the barn, as indicated by a mercurial thermometer, was recorded simultaneously with every observation on the body temperature of the animal.

METHOD OF MAKING BODY-TEMPERATURE OBSERVATIONS

The observations on the body temperature were made by means of carefully standardized clinical thermometers. During the greater part of the experiment one and the same thermometer was used, while for simultaneous readings of the rectal and vaginal temperatures a second one was used. To avoid any possible error as to the relative value of the rectal and vaginal temperatures that might be due to the use of two different thermometers, the latter were for a few days interchanged—that is, the thermometer used one day for measuring the rectal temperature was used the following day for the vaginal, and vice versa. This was further checked by using one and the same thermometer for both the rectal and vaginal temperature readings, taken one immediately after the other.

All observations except those on the thermal gradient were made at a depth of 7 inches. The thermometers, which were originally 5 inches long, were accordingly lengthened by means of a piece of rubber tubing slipped ½ inch or so over the upper end of the thermometer and the

remaining portion over the string attached to the loop of the thermometer and stiffened by inserting inside the rubber tubing a strip of copper wire. This was finally covered with adhesive plaster and a rubber ring tightly fitted at the end. This arrangement proved very satisfactory. In the first place, the thermometer could be inserted to the desired depth, and, in the second place, there was little danger of breaking it during the insertion.

The thermometer was ordinarily allowed to stay in the rectum or vagina for about three minutes, and the time and temperature were recorded immediately upon its removal.

EXPERIMENTAL RESULTS

The results are expressed in the form of curves. In all curves except those of the thermal gradient the hours or dates are expressed by horizontal distances, and the corresponding temperatures are represented vertically. In the curves of the thermal gradient the horizontal dis-

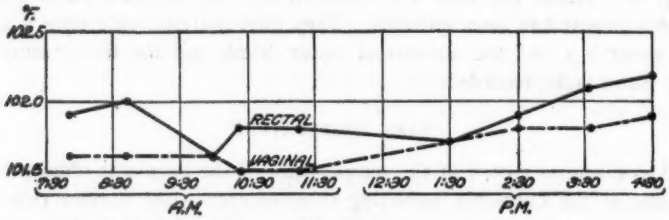


FIG. 1.—Variations in body temperature of cow 886 on December 1, 1919, 7.50 a. m. to 4.30 p. m.; 7.50 a. m. immediately after urinating; 8.25 a. m. drank 5.2 kgm. of water at 52° F.; 10 a. m. lying; 10.22 a. m. standing and immediately after defecating; 11.15 a. m. lying; 1.30 p. m. lying; 2.30 to 4.30 p. m. standing; 3.32 p. m. immediately after defecating.

tances represent the depths of insertion, and the vertical distances represent the corresponding temperatures.

The barn temperatures are not given because they were too uniform to have had any appreciable effect on the body temperature, ranging in most cases between 50° to 60° F.

To facilitate comparisons, the different types of curves for the two cows have been arranged to follow each other in more or less chronological order.

VARIATIONS IN BODY TEMPERATURE FROM ABOUT 7.30 A. M. TO ABOUT 5.30 P. M.

OBSERVATIONS ON DECEMBER 1, 1919, WITH COW 886

Readings of the rectal and vaginal temperatures were taken at approximately 1-hour intervals from 7.50 a. m. to 11.15 a. m. and from 1.30 p. m. to 4.30 p. m. The vaginal temperature was measured immediately after the rectal by the same thermometer. The reading of the vaginal temperature at 7.50 a. m. was taken immediately after the cow had

urinated. At 8.25 a. m. the cow drank 5.2 kgm. of water at 52° F. During the observations at 10 a. m., 11.15 a. m., and 1.30 p. m. the cow was lying; during all others she was standing. The readings at 10.22 a. m. and 3.32 p. m. were taken immediately after the animal had defecated. The results of these observations are shown in figure 1.

The curve for the rectum shows a slight fall in temperature between 8.40 a. m. and 10 a. m., the period following the drinking of the water. It then slightly rises and from 10.22 a. m. to 1.30 p. m. forms almost a straight line. From 1.30 p. m. to 4.30 p. m. it shows a gradual rise of temperature.

The curve for the vagina is in general lower than that for the rectum. It does not show, however, any effect of the water drunk, forming a straight line till 10 a. m. and meeting the rectal curve at that time. The two curves then diverge to meet again at 1.30 p. m. They then diverge again but soon run almost parallel to each other till 4.30 p. m.

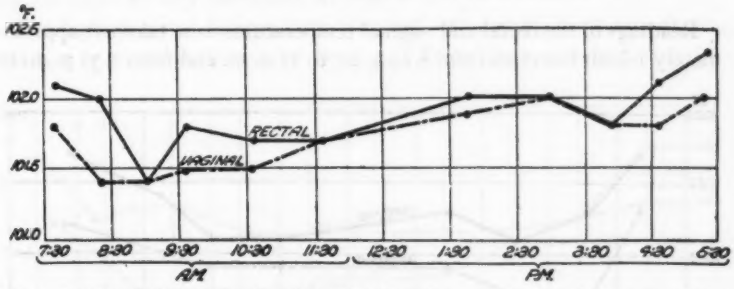


FIG. 2.—Variations in body temperature of cow 886 on December 2, 1919, 7.40 a. m. to 5.20 p. m. At 7.40 a. m. standing; 8.00 a. m. drank 13.0 kgm. of water at 48° F.; 8.20 a. m. lying; 9.00 a. m standing and immediately after defecating; 9.35 a. m. to 10.35 a. m. lying; 2.57 p. m. standing; 3.55 p. m. lying down with thermometers inserted; 4.35 p. m. immediately after defecating; 5 p. m. to 5.20 p. m. eating.

The highest rectal temperature obtained was 102.2° F. at 4.30 p. m., while the lowest was 101.6° at 10 a. m. The highest vaginal temperature obtained was 101.9° at 4.30 p. m., while the lowest was 101.5° at 10.22 a. m. and 11.15 a. m.

OBSERVATIONS ON DECEMBER 2, 1919, WITH COW 886

Readings of the rectal and vaginal temperatures were taken at approximately 1-hour intervals from 7.40 a. m. to 11.35 a. m. and from 1.50 to 5.20 p. m. The rectal and vaginal temperatures were measured at the same time by the two thermometers. At 8 a. m. the cow drank 13 kgm. of water at 48° F. During the observations at 8.20 a. m., 9.35 a. m., and 10.35 a. m. the cow was lying; at 3.55 p. m. the cow lay down with the thermometers inserted. The cow was up during all the other readings. At 9 a. m. and at 4.35 p. m. the readings were taken immediately after defecation. The cow was fed at 5 p. m., and at the end of the observations—that is, at 5.20 p. m.—she was still eating. The results are given in figure 2.

The curve for the rectum, as in figure 1, shows a fall in temperature during the period following the drinking of the water. This drop is, however, more sudden and more noticeable, presumably on account of the greater amount of water drunk. The curve is quite uniform from 9.35 a. m. to 2.57 p. m., when it shows again a fall in temperature till 3.55 p. m., followed by a rise till 5.20 p. m.

The curve for the vagina is again lower than that for the rectum. It shows the effect of the water a little earlier than the rectal. During their course the two curves meet four times. There is, in general, however, some resemblance between figure 1 and figure 2.

The highest rectal temperature obtained was 102.3° F. at 5.20 p. m., while the lowest was 101.4° at 9 a. m. The highest vaginal temperature obtained was 102° at 5.20 p. m., while the lowest was 101.4° at 8.20 a. m. and at 9 a. m.

OBSERVATIONS ON DECEMBER 3, 1919, WITH COW 886

Readings of the rectal and vaginal temperatures were taken at approximately 1-hour intervals from 8.10 a. m. to 11 a. m. and from 1.30 p. m. to

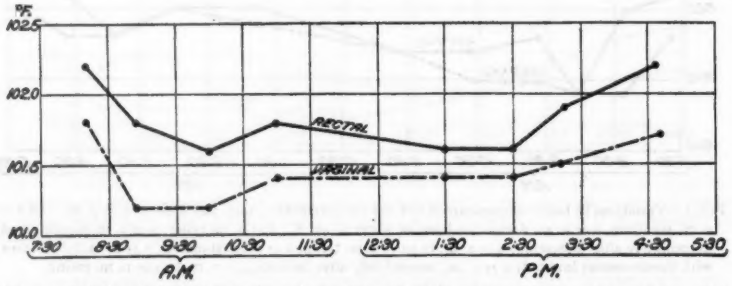


FIG. 3.—Variations in body temperature of cow 886 on December 3, 1919, 8.10 a. m. to 4.36 p. m. At 8 a. m. drank 13.0 kgm. of water at 55° F.; 8.10 a. m. to 8.54 a. m. standing; 10 a. m. immediately after getting up and defecating; 11 a. m. lying; 1.30 p. m. to 4.46 p. m. standing; 3.15 p. m. immediately after defecating; 4.36 p. m. immediately after defecating.

4.36 p. m. The rectal and vaginal temperatures were measured simultaneously by means of the two thermometers interchanged—that is, the one used on December 2 for the rectum was used here for the vagina, and vice versa. At 8 a. m. the cow drank 13 kgm. of water at 55° F. At 11 a. m. the cow was lying. During all other observations the cow was up. The readings at 10 a. m., 3.15 p. m., and 4.36 p. m. were taken immediately after defecation. The results of these observations are given in figure 3.

The curves show the usual fall in temperature after watering and the rise in temperature in the afternoon. The curve for the vagina is lower than that for the rectum and is to a great degree parallel with it.

The highest rectal temperature obtained was 102.2° F. at 8.10 a. m. and 4.36 p. m., while the lowest was 101.6° at 10 a. m. and 2.30 p. m. The

highest vaginal temperature obtained was 101.8° at 8.10 a. m., while the lowest was 101.2° at 8.54 a. m. and at 10 a. m.

OBSERVATIONS ON DECEMBER 4, 1919, WITH COW 886

Observations on the rectal and vaginal temperatures were made at approximately 1-hour intervals from 7.45 a. m. to 5.24 p. m. The rectal and vaginal temperatures were measured simultaneously with the two thermometers, as on the preceding day. At 8.05 a. m. the cow drank 9 kgm. of water at 54° F. During the readings at 8.57 a. m. and 2.24 p. m. the cow was lying, while during all others she was standing. At 9.33 a. m. the reading was taken immediately after defecation. From 5 p. m. to 5.24 p. m. the cow was eating. The results are represented by figure 4.

The curves show the usual fall in temperature after watering and the rise in the afternoon. The vaginal curve is lower than the rectal, meeting the latter at only one point, at 3.30 p. m.

The highest rectal temperature obtained was 102.2° F. at 4.24 p. m. and 5.24 p. m., while the lowest was 101.6° from 10.42 a. m. to 2.24 p. m.

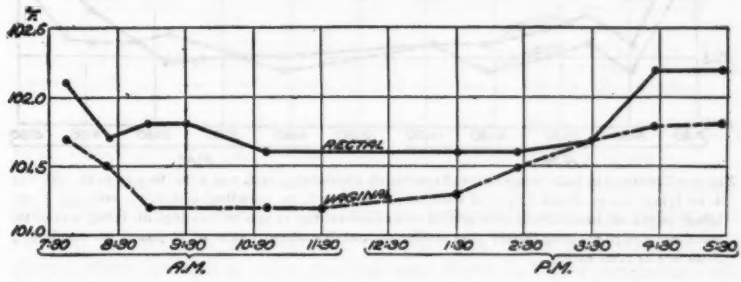


FIG. 4.—Variations in body temperature of cow 886 on December 4, 1919, 7.45 a. m. to 5.24 p. m. From 7.45 a. m. to 8.24 a. m. standing; 8.05 a. m. drank 9 kgm. of water at 54° F.; 8.57 a. m. lying; 9.33 a. m. immediately after getting up and defecating; 10.42 a. m. to 1.30 p. m. standing; 2.24 p. m. lying; 3.30 p. m. to 5.24 p. m. standing; 5 p. m. to 5.24 p. m. eating.

The highest vaginal temperature obtained was 101.8° at 4.24 p. m. and 5.24 p. m., while the lowest was 101.2° from 8.57 a. m. to 11.30 a. m.

OBSERVATIONS ON DECEMBER 5, 1919, WITH COW 886

Observations on the rectal and vaginal temperatures were made at approximately 1-hour intervals from 7.45 a. m. to 11.24 a. m. and from 1.36 p. m. to 5.24 p. m. The rectal and vaginal temperatures were measured at the same time with the two thermometers as on December 2 (fig. 2). At 8 a. m. the cow drank 6 kgm. of water at 54° F. At 7.45 a. m., 9.42 a. m., 11.24 a. m., and 1.36 p. m. the cow was lying; during the other readings she was standing. At 10.36 a. m. and at 3.18 p. m. the readings were taken immediately after defecation. From 5 p. m. to 5.24 p. m. the cow was eating. The results are represented by figure 5.

The peculiar feature of these curves is that the vaginal curve crosses the rectal at two points, besides meeting at another. The usual fall in temperature after watering and the rise in the afternoon are also shown.

The highest rectal temperature obtained was 102.3° F. at 7.45 a. m., while the lowest was 101.45° at 3.18 p. m. The highest vaginal temperature obtained was 102° at 7.45 a. m. and 5.24 p. m., while the lowest was 101.4° at 8.27 a. m., 10.36 a. m., and 1.36 p. m.

OBSERVATIONS ON DECEMBER 1, 1919, WITH COW 885

Observations on the rectal and vaginal temperatures were made at approximately 1 hour intervals from 8.06 a. m. to 11.30 a. m. and from 1.30 p. m. to 4.30 p. m. The vaginal temperature was measured immediately after the rectal by the same thermometer. At 8.30 a. m. the cow drank 29.4 kgm. of water at 52° F. The cow was standing during

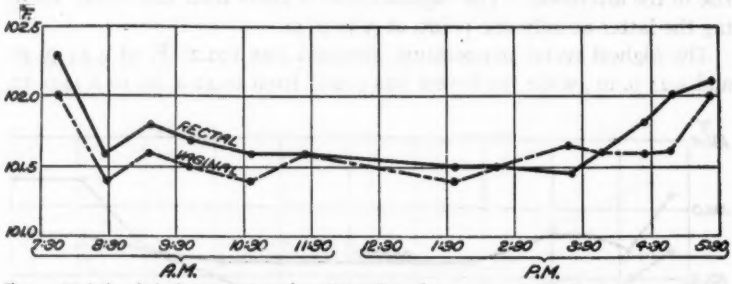


FIG. 5.—Variations in body temperature of cow 886 on December 5, 1919, 7.45 a. m. to 5.24 p. m. At 7.45 a. m. lying; 8 a. m. drank 6 kgm. of water at 54° F.; 8.27 a. m. standing; 9.06 a. m. and 9.42 a. m. lying; 10.36 a. m. immediately after getting up and defecating; 11.24 a. m. to 1.36 p. m. lying; 2.15 p. m. standing; 3.18 p. m. immediately after getting up and defecating; 3.42 p. m. to 5.24 p. m. standing; 5 p. m to 5.24 p. m. eating.

all readings. At 8.12 a. m., 10.12 a. m., and 2.30 p. m. the readings were taken immediately after defecation. The results are represented by figure 6.

The peculiar feature of these curves is the very marked effect of the large quantity of water drunk. The vaginal is lower than the rectal curve and is almost parallel with it, meeting it, however, at two points. The usual rise in temperature in the afternoon is also shown.

The highest rectal temperature obtained was 102.2° F. at 4.30 p. m., while the lowest was 100.2° at 10.12 a. m. The highest vaginal temperature obtained was 101.7° at 8.12 a. m., while the lowest was 100.2° at 10.12 a. m.

OBSERVATIONS ON DECEMBER 2, 1919, WITH COW 885

Readings of the rectal and vaginal temperatures were taken at approximately 1-hour intervals from 7.48 a. m. to 10.45 a. m. and from 2 p. m. to 5.30 p. m. The rectal and vaginal temperatures were measured at the same time with the two thermometers as for figures 2 and 5. At

about 8 a. m. the cow was offered water, but she refused to drink. At 7.48 a. m. the cow was lying; during all other readings she was standing. At 9.25 a. m. the reading was taken immediately after the cow had urinated. At 7.48 a. m., 3.10 p. m., 5 p. m., and 5.30 p. m. the read-

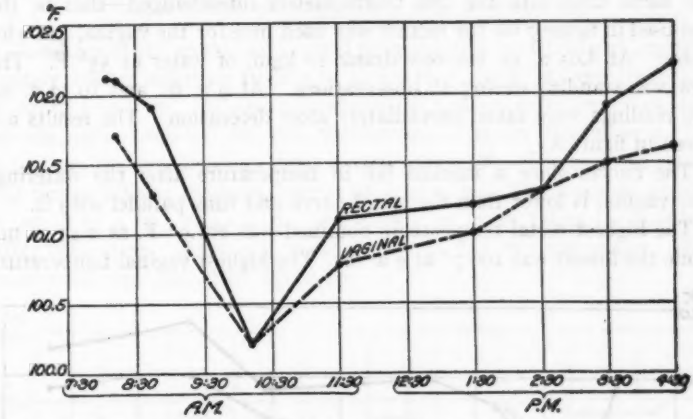


FIG. 6.—Variations in body temperature of cow 885 on December 1, 1919, 8.06 a. m. to 4.30 p. m. From 8.06 a. m. to 4.30 p. m. standing; 8.12 a. m. immediately after defecating; 8.30 a. m. drank 29.4 kgm. of water at 52°F.; 10.12 a. m. immediately after urinating and defecating; 2.30 p. m. after defecating.

ings were taken immediately after defecation. From 5 p. m. to 5.30 p. m. the cow was eating. The results are represented by figure 7.

The striking feature of these curves is that they are very much smoother than the preceding ones. The drop in temperature in the morning is lacking, apparently, because the cow did not drink any water. The curves show instead a very gradual and slight fall in temperature till

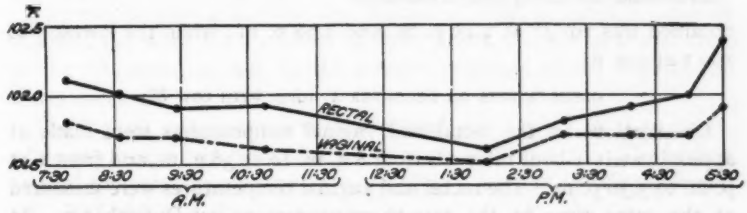


FIG. 7.—Variations in body temperature of cow 885 on December 2, 1919, 7.48 a. m. to 5.30 p. m. At 7.48 a. m. lying and immediately after defecating; 8.36 a. m. to 5.30 p. m. standing; cow drank no water; 9.25 a. m. immediately after urinating; 3.10 p. m. immediately after defecating; 5 p. m. immediately after defecating; 5 p. m. to 5.30 p. m. eating; 5.30 p. m. immediately after defecating.

2 p. m., and from that time a gradual rise. The vaginal curve is lower than the rectal and runs almost parallel with it, not meeting it at any point.

The highest rectal temperature obtained was 102.4° F. at 5.30 p. m., while the lowest was 101.6° at 2 p. m. The highest vaginal temperature obtained was 101.9° at 5.30 p. m., while the lowest was 101.5° at 2 p. m.

OBSERVATIONS ON DECEMBER 3, 1919, WITH COW 885

Readings of the rectal and vaginal temperatures were taken at approximately 1-hour intervals from 8.20 a. m. to 11.12 a. m. and from 1.38 p. m. to 4.48 p. m. The rectal and vaginal temperatures were measured at the same time with the two thermometers interchanged—that is, the one used in figure 7 for the rectum was used here for the vagina, and vice versa. At 8.05 a. m. the cow drank 22 kgm. of water at 55° F. The cow was standing during all observations. At 9 a. m. and 10.12 a. m. the readings were taken immediately after defecation. The results are given in figure 8.

The curves show a marked fall in temperature after the watering. The vaginal is lower than the rectal curve and runs parallel with it.

The highest rectal temperature obtained was 101.9° F. at 2.45 p. m., while the lowest was 100.7° at 9 a. m. The highest vaginal temperature

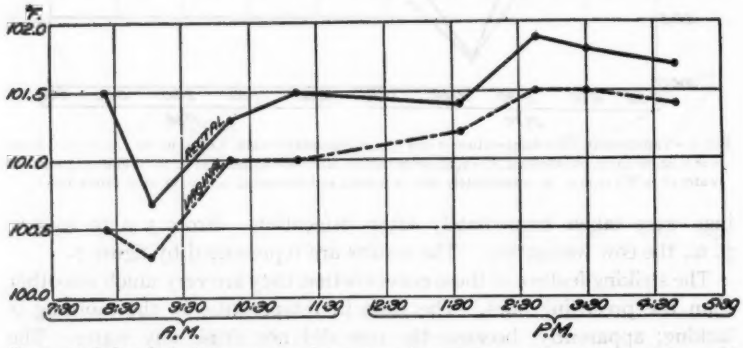


FIG. 8.—Variations in body temperature of cow 885 on December 3, 1919, 8.20 a. m. to 4.48 p. m. At 8.05 a. m. drank 22 kgm. of water at 55° F.; 9 a. m. immediately after defecating; 10.12 a. m. immediately after defecating; cow standing during all observations.

obtained was 101.5° at 2.45 p. m. and 3.30 p. m., while the lowest was 100.3 at 9 a. m.

OBSERVATIONS ON DECEMBER 4, 1919, WITH COW 885

Observations on the rectal and vaginal temperatures were made at approximately 1-hour intervals from 8 a. m. to 11.36 a. m. and from 1.42 p. m. to 5.30 p. m. The rectal and vaginal temperatures were measured at the same time by the two thermometers as on December 3. At about 8 a. m. the cow was offered water, but she refused to drink. At 10.54 a. m. the cow was lying; during all other observations she was standing. At 9.12 a. m. and 4.45 p. m. the readings were taken immediately after defecation. From 5 p. m. to 5.30 p. m. the cow was eating. The results are represented by figure 9.

The curves show irregularity for the first three hours but are much smoother for the rest of the day. Although meeting each other at the very start, the curves soon diverge and the vaginal remains considerably lower than the rectal throughout their course.

The highest rectal temperature obtained was 102.2° F. at 5.30 p. m., while the lowest was 101.6° at 8 a. m. The highest vaginal temperature obtained was 101.8° at 5.30 p. m., while the lowest was 101.2° at 9.12 a. m., 11.36 a. m., and 1.42 p. m.

OBSERVATIONS ON DECEMBER 5, 1919, WITH COW 885

Readings of the rectal and vaginal temperatures were taken at approximately 1-hour intervals from 7.57 a. m. to 11.30 a. m. and from 1.48 p. m. to 5.30 p. m. The rectal and vaginal temperatures were measured at the same time by the two thermometers as on December 2. At 8.10 a. m. the cow drank 23 kgm. of water at 54° F. The cow was standing during all the readings, except at 9.30 a. m. The readings at 7.57 a. m., 8.45 a. m., 10.42 a. m., and 5.30 p. m. were taken immediately after defecation. From 5 p. m. to 5.30 p. m. the cow was eating. The results are represented by figure 10.

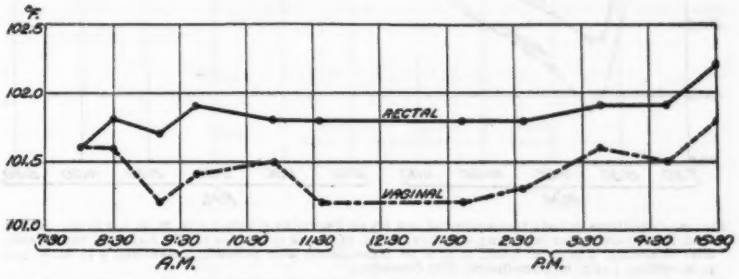


FIG. 9.—Variations in body temperature of cow 885 on December 4, 1919, 8 a. m. to 5.30 p. m. Cow drank no water; 8 a. m. immediately after defecating, standing; 9.12 a. m. immediately after defecating, standing; 10.54 a. m. lying; 11.36 a. m. to 5.30 p. m. standing; 4.45 p. m. immediately after defecating; 5 p. m. to 5.30 p. m. eating.

The curves show a striking resemblance to those in figure 6, showing in about the same way the effect of water drunk, the rise in temperature in the afternoon, as well as the relative positions of the vaginal and rectal curves.

The highest rectal temperature obtained was 102° F. at 5.30 p. m., while the lowest was 100.4° from 8.45 a. m. to 8.56 a. m. The highest vaginal temperature obtained was 101.6° at 5.30 p. m., while the lowest was 99.9° at 8.56 a. m.

GENERAL CONCLUSIONS WITH REGARD TO THE VARIATIONS IN BODY TEMPERATURE FROM ABOUT 7.30 A. M. TO ABOUT 5.30 P. M.

All the foregoing observations indicate that, in cows, the vaginal temperature is decidedly lower than the rectal, when measured at the same depth of 7 inches, while a trend toward parallelism between the two is also apparent. This can be, at least partially, explained by the fact that the vagina is more exposed to the outside atmosphere than is the rectum. For determinations of the average body temperature the

rectum, therefore, is to be preferred to the vagina as a place for inserting the thermometer.

A fall in temperature invariably follows the drinking of water. This fall varies with the quantity of water drunk. Consequently, the first two or three hours after watering do not afford a good time for comparative determinations of body temperature.

After the body has overcome the effect of the water, the temperature appears quite uniform for about three hours, after which there is a gradual

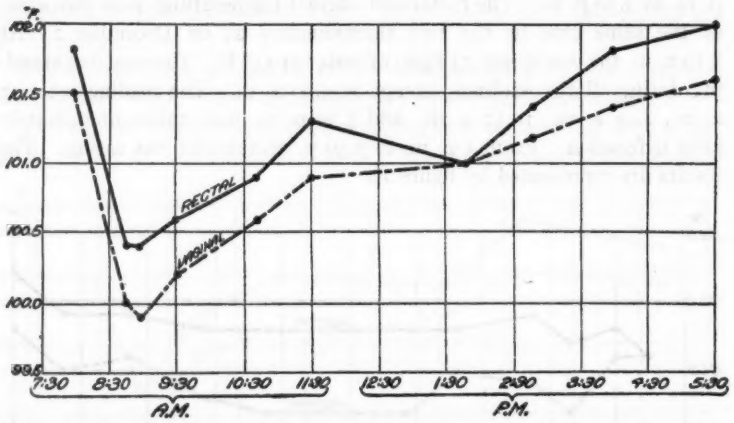


FIG. 10.—Variations in body temperature of cow 885 on December 5, 1919, 7.57 a. m. to 5.30 p. m. At 7.57 a. m. immediately after defecating, standing; 8.10 a. m. drank 23 kgm. at 54° F.; 8.45 a. m. immediately after defecating; 9.30 a. m. lying; 10.42 a. m. immediately after defecating, standing; 5 p. m. to 5.30 p. m. eating; 5.30 p. m. immediately after defecating.

rise which reaches its maximum at about 5.30 p. m. The accelerated rise, however, from 5 p. m. to 5.30 p. m. may be due to the eating.

Since the exact time when the animal changed its position was not recorded during these observations, no definite conclusions can be drawn as to what effect the position of the animal has on the body temperature.

The act of defecation did not produce any noticeable effect.

The highest rectal temperature obtained during this series of observations was 102.4° F. at 5.30 p. m. (fig. 7). The lowest rectal temperature was 100.2° at 10.12 a. m. (fig. 6). The highest vaginal temperature obtained was 102° at 2.57 p. m., 5.20 p. m. (fig. 2), and 5.24 p. m. (fig. 5), while the lowest was 99.9° at 8.56 a. m. (fig. 10).

OBSERVATIONS ON THE THERMAL GRADIENT

Recent investigations on the body temperature of man[1] and other animals[2] show that variations in body temperature depend to a very great extent on the depth to which the thermometer is inserted, and that

[1] BENEDICT, Francis G., and SLACK, Edgar P. A COMPARATIVE STUDY OF TEMPERATURE FLUCTUATIONS IN DIFFERENT PARTS OF THE HUMAN BODY. V, 73 p., illus. Washington, D. C., 1911. (Carnegie Inst. Washington Pub. 155.)

[2] LIPSCHÜTZ, Alexander. ÜBER DIE ABHÄNGIGKEIT DER KÖRPERTEMPERATUR VON DER PUBERTÄTSDRÜSE. In Arch. Gesam. Physiol., Bd. 168, Heft 1/4, p. 177–192, 1 fig. 1917.

the thermal gradient rises sharply for the first few centimeters beneath the surface of the skin and soon reaches a point beyond which the body temperature is not materially increased. To reach this point in man[1] and in the guinea pig[2] 6 or 7 cm. were found to be sufficient. The following observations were made with the view of testing out these findings on cows.

OBSERVATIONS ON THERMAL GRADIENT, WITH COW 886 ON DECEMBER 5, 1919, 2.09 P. M. TO 3.18 P. M.

Observations on the rectal and vaginal temperatures were made simultaneously with the two thermometers. The thermometers were first inserted 4 inches deep, then 5 inches, then 7 inches, then 6 inches, and finally again 7 inches. The results are represented by figure 11, and the actual temperature observations, the time, and the insertions are given in Table I.

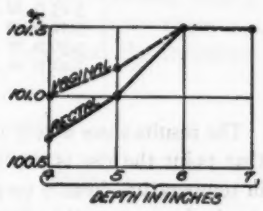


FIG. 11.—Observations on thermal gradient with cow 886 on December 5, 1919, 2.09 p. m. to 3.18 p. m.

TABLE I.—*Thermal gradient observations*

Time.	Rectal temperature.	Vaginal temperature.	Depth inserted.
	°F.	°F.	*Inches.*
2.09 p. m...	100. 7	101. 0	4
2.12 p. m...	101. 0	101. 2	5
2.15 p. m...	101. 5	101. 5	7
2.24 p. m...	101. 5	101. 5	6
3.18 p. m...	101. 5	.....	7

The results show that at a depth of 4 inches the rectal temperature was 0.80° F. lower than at a depth of either 6 or 7 inches, while it was only 0.3° lower than at a depth of 5 inches. The vaginal temperature was 0.2° lower at a depth of 4 inches than at a depth of 5 inches and 0.5° lower than at a depth of either 6 or 7 inches. There was no rise in temperature between 6 and 7 inches—that is, the maximum body temperature was reached in this case when the thermometer was inserted 6 or 7 inches into the rectum or the vagina. Up to a depth of 6 inches the vaginal curve appears higher than the rectal.

OBSERVATIONS ON THERMAL GRADIENT, WITH COW 886, ON DECEMBER 5, 1919, 3.25 P. M. TO 3.42 P. M.

Readings of the rectal and vaginal temperatures were taken simultaneously as before. The thermometers were first inserted 6 inches deep, then 5 inches, then 4 inches, and finally 7 inches. The results are represented by figure 12, and the actual temperature observations, the time and the insertions are given in Table II.

[1] BENEDICT, Francis G., and SLACK, Edgar P. OP. CIT.
[2] LIPSCHUTZ, Alexander. OP. CIT.

TABLE II.—*Thermal gradient observations*

Time.	Rectal temperature.	Vaginal temperature.	Depth inserted.
	° *F.*	° *F.*	*Inches.*
3.25 p. m...	101. 4	101. 5	6
3.30 p. m...	101. 2	101. 5	5
3.36 p. m...	100. 5	101. 2	4
3.42 p. m...	101. 6	101. 6	7

The results show a very rapid rise between 4 and 5 inches, while beyond that point the rise is much slower. In this case there was a slight rise in temperature from 6 to 7 inches. However, it is very likely that this rise is due not to this difference in depth but to the difference in time, since there was an interval of 17 minutes between the two readings and the tendency of the body temperature is to rise in the afternoon. The vaginal curve is higher than the rectal, but they meet at a depth of 7 inches.

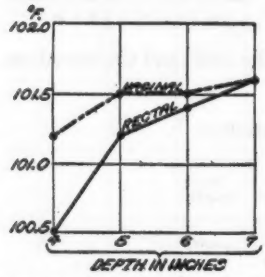


FIG. 12.—Observations on thermal gradient with cow 886 on December 5, 1919, 3.25 p. m. to 3.42 p. m.

OBSERVATIONS ON THERMAL GRADIENT WITH COW 885 ON DECEMBER 5, 1919, 4 P. M. TO 4.18 P. M.

Readings of the rectal and vaginal temperatures were taken simultaneously by the two thermometers as before. The thermometers were inserted first 6 inches deep, then 7 inches, then 4 inches, and finally 5 inches. The results are represented by figure 13, and the actual temperature observations, the time, and the insertions are given in Table III.

TABLE III.—*Thermal gradient observations*

Time.	Rectal temperature.	Vaginal temperature.	Depth inserted.
	° *F.*	° *F.*	*Inches.*
4.00 p. m.....	101. 7	101. 3	6
4.03 p. m.....	101. 8	101. 4	7
4.10 p. m.....	101. 4	101. 0	4
4.18 p. m.....	101. 5	101. 2	5

The results show a very gradual rise from 4 inches to 7 inches, the difference being only 0.4° F. The order in which the readings were taken is significant in showing that despite the tendency of the body temperature to rise at this time of the day, the 4- and 5-inch insertions which followed the 6- and 7-inch insertions show a lower temperature than the latter. The vaginal curve is in this case lower than the rectal and is parallel with it.

OBSERVATIONS ON THERMAL GRADIENT WITH COW 886 ON DECEMBER 5, 1919, 4.24 P. M. TO 4.42 P. M.

Observations on the rectal and vaginal temperatures were made simultaneously by means of the two thermometers as before. The thermometers were first inserted 7 inches deep, then 6 inches, then 5 inches, and finally 4 inches. The results are represented by figure 14, and the actual temperature observations, the time, and the insertions are given in Table IV.

TABLE IV.—*Thermal gradient observations*

Time.	Rectal temperature.	Vaginal temperature.	Depth inserted.
	° *F.*	° *F.*	*Inches.*
4.24 p. m.....	101. 8	101. 6	7
4.30 p. m.....	101. 8	101. 6	6
4.36 p. m.....	101. 7	101. 5	5
4.42 p. m.....	101. 5	101. 2	4
4.48 p. m.....	102. 0	101. 6	7

The results show a more rapid rise in temperature from a depth of 4 to 5 inches than from 5 to 6 inches. There is no change in temperature from a depth of 6 to a depth of 7 inches, thus indicating that the maximum

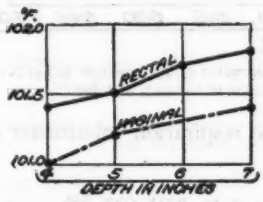


FIG. 13.—Observations on thermal gradient with cow 885 on December 5, 1919, 4 p. m. to 4.18 p. m.

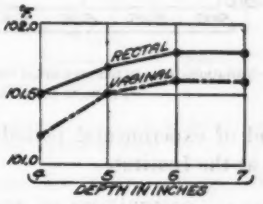


FIG. 14.—Observations on thermal gradient with cow 886 on December 5, 1919, 4.24 p. m. to 4.42 p. m.

temperature was in this case reached at a depth of 6 inches. The reading at 4.48 p. m. is given in the table to show the effect of the time of day. The vaginal curve is lower than the rectal and is parallel with it.

GENERAL CONCLUSIONS WITH REGARD TO THE THERMAL GRADIENT

From a consideration of the results given above it is apparent that the thermal gradient between the temperature at a depth of 4 inches and at a depth of 6 inches is noticeable, while there is no material change between a depth of 6 inches and a depth of 7 inches. It may be concluded, therefore, that at a depth of 7 inches the body temperature is essentially at its maximum. This does not show, of course, that the temperature may not be actually higher in some other parts of the body, where there is a specific metabolic activity, but it does show that it is

much safer in the determinations of the average body temperature of a cow to insert the thermometer to a depth of 7 inches than to a depth of 4 or 5 inches.

The fact that the vaginal curve below 6 or 7 inches is in some cases higher than the rectal (fig. 11, 12) and in some cases lower (fig. 13, 14) illustrates the inconstancy of the temperature when measured at a depth below 6 inches.

VARIATIONS IN BODY TEMPERATURE FROM ABOUT 5 P. M. TO ABOUT 7 P. M.

The purpose of making temperature observations from about 5 p. m. to about 7 p. m. is twofold: First, to study the effect of the feed on the body temperature and, second, to get some idea as to the temperature fluctuations at 6 p. m., the time representing the beginning as well as

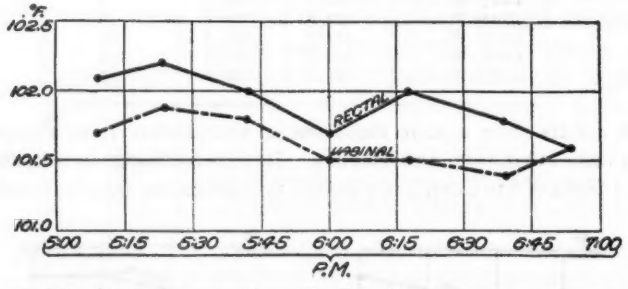


FIG. 15.—Variations in body temperature of cow 886 on December 9, 1919, 5.10 p. m. to 6.54 p. m. From 5 p. m. to 5.42 p. m. eating; 6.18 p. m. to 6.54 p. m. lying.

the end of experimental periods in the respiration calorimeter experiments at the Institute.

OBSERVATIONS ON DECEMBER 9, 1919, WITH COW 886

Observations on the rectal and vaginal temperatures were made at approximately 15-minute intervals from 5.10 p. m. to 6.54 p. m. The cow was eating from 5 p. m. to 5.42 p. m. From 6.18 p. m. to 6.54 p. m. she was lying. The results are represented by figure 15.

The curves show a slight rise in temperature from 5.10 p. m. to 5.25 p. m., followed by a gradual fall till 6 p. m. After 6 p. m. the rectal curve again shows a rise till 6.18 p. m., followed by a gradual drop till 6.54 p. m., when it meets the vaginal curve. The vaginal curve is lower than the rectal and is parallel with it only till 6 p. m.

OBSERVATIONS ON DECEMBER 10, 1919, WITH COW 886

Readings of the rectal and vaginal temperatures were taken at approximately 15-minute intervals from 5 p. m. to 6.30 p. m. From 5 p. m. to 5.36 p. m. the cow was eating. The reading at 5 p. m. was taken immediately after defecation. The cow was lying from 6.03 p. m. to 6.30 p. m. The results are given in figure 16.

The curves show, in general, a slight and gradual drop. It should be noted that the initial temperature—that is, the temperature at 5 p. m.—was rather high.

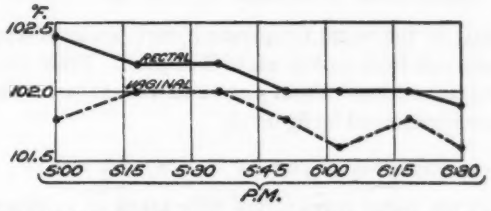


FIG. 16.—Variations in body temperature of cow 886 on December 10, 1919, 5 p. m. to 6.30 p. m. From 5 p. m. to 5.36 p. m. eating; 5 p. m. immediately after defecating; 6.03 p. m. to 6. 30 p. m. lying.

OBSERVATIONS ON DECEMBER 11, 1919, WITH COW 886

Readings of the rectal and vaginal temperatures were taken at approximately 15-minute intervals from 4.52 p. m. to 6.36 p. m. From 5 p. m. to 5.48 p. m. the cow was eating. From 6.21 p. m. to 6.36 p. m. she was lying. The results are represented by figure 17.

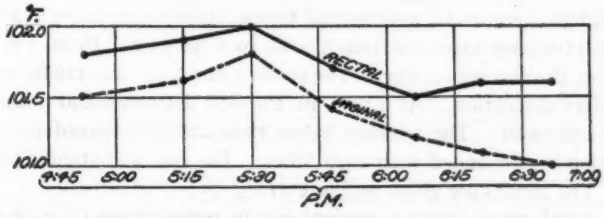


FIG. 17.—Variations in body temperature of cow 886 on December 11, 1919, 4.52 p. m. to 6.36 p. m. From 5 p. m. to 5.48 p. m. eating; 6.21 p. m. to 6.36 p. m. lying.

The curves show a gradual rise in temperature till 5.30 p. m., followed by a fall which is continuous in the vaginal temperature but is interrupted by a very slight rise in the rectal temperature at 6.21 p. m., the time the cow lay down. The two curves are nearly parallel.

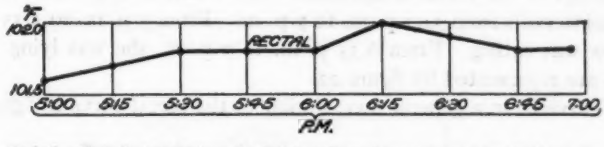


FIG. 18.—Variations in body temperature of cow 886 on December 13, 1919, 5 p. m. to 6.57 p. m. From 5 p. m. to 5.30 p. m. eating; 6.15 p. m. to 6.57 p. m. lying.

OBSERVATIONS ON DECEMBER 13, 1919, WITH COW 886

Observations on the rectal temperature were made at about 15-minute intervals from 5 p. m. to 6.57 p. m. From 5 p. m. to 5.30 p. m. the cow was eating. From 6.15 p. m. to 6. 57 p. m. she was lying. The results are given in figure 18.

The curve shows, in general, a gradual rise till 6.15 p. m., the time the cow lay down, followed by a slight and gradual drop.

OBSERVATIONS ON DECEMBER 14, 1919, WITH COW 886

Observations on the rectal temperature were made at approximately 15-minute intervals from 5.06 p. m. to 6.21 p. m. From 5 p. m. to 5.36 p. m. the cow was eating. From 5.50 p. m. to 6.21 p. m. she was lying. The results are represented by figure 19.

OBSERVATIONS ON JANUARY 12, 1920, WITH COW 886

Readings of the rectal temperature were taken at 15-minute intervals from 5 p. m. to 6 p. m. The cow was eating from 5 p. m. to 6. p. m. The results are given in figure 20.

The curve shows, in general, a gradual rise from 5 p. m. to 6 p. m. It should be mentioned that the cow received a supermaintenance ration at this date and that she spent the whole hour from 5 p. m. to 6 p. m. in eating.

OBSERVATIONS ON DECEMBER 11, 1919, WITH COW 885

Readings of the rectal and vaginal temperatures were taken at approximately 15-minute intervals from 5 p. m. to 6. 30 p. m. From 5 p. m. to 5.42 p. m. the cow was eating. The reading at 5 p. m. was taken immediately after defecation. At 6.15 p. m. the cow defecated and pushed out the thermometer. The readings taken then and also immediately after defecation corresponded with each other. The cow was standing all the time. The results are given in figure 21.

The rectal curve shows a gradual rise in temperature till 5.42 p. m., the time the cow was through eating, followed by a slight fall in temperature till 6.15 p. m., followed again by a rise. The vaginal curve is much lower than the rectal.

OBSERVATIONS ON DECEMBER 13, 1919, WITH COW 885

Readings of the rectal temperature were taken at approximately 15-minute intervals from 5.12 p. m. to 7 p. m. From 5 p. m. to 5.35 p. m. the cow was eating. From 6.35 p. m. to 7 p. m. she was lying. The results are represented by figure 22.

The curve is, in a general way, similar to the rectal curve in figure 21.

OBSERVATIONS ON DECEMBER 14, 1919, WITH COW 885

Observations on the rectal temperature were made at approximately 15-minute intervals from 5.18 p. m. to 6.12 p. m. From 5 p. m. to 5.35 p. m. the cow was eating. The cow was up all the time. The results are given in figure 23.

The peculiar feature of this curve is the rather rapid drop from 5.30 p. m. to 6.12 p. m.

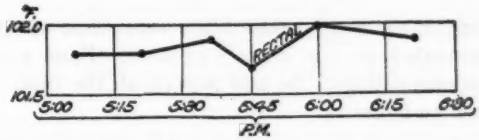


FIG. 19.—Variations in body temperature of cow 886 on December 14, 1919, 5.06 p. m. to 6.21 p. m. From 5 p. m. to 5.36 p. m. eating; 5.50 p. m. to 6.21 p. m. lying.

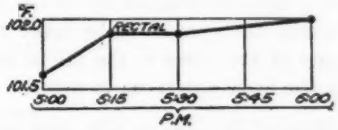


FIG. 20.—Variations in body temperature of cow 886 on January 12, 1920, 5 p. m. to 6 p. m. From 5 p. m. to 6 p. m. eating.

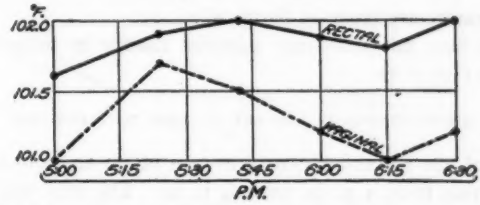


FIG. 21.—Variations in body temperature of cow 885 on December 11, 1919, 5 p. m. to 6.30 p. m. From 5 p. m. to 5.42 p. m. eating; 5 p. m. immediately after defecating; 6.15 p. m. immediately before and after defecating; cow standing all the time.

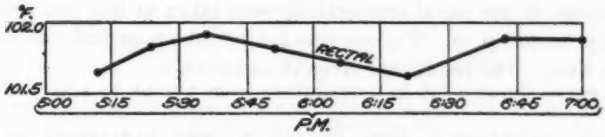


FIG. 22.—Variations in body temperature of cow 885 on December 13, 1919, 5.12 to 7 p. m. From 5 p. m. to 5.35 p. m. eating; 6.35 p. m. to 7 p. m. lying.

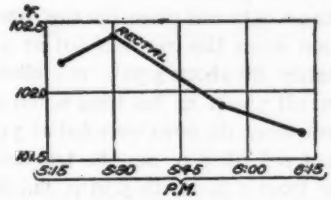


FIG. 23.—Variations in body temperature of cow 885 on December 14, 1919, 5.18 p. m. to 6.12 p. m. From 5 p. m. to 5.35 p. m. eating; cow standing all the time.

OBSERVATIONS ON JANUARY 4, 1920, WITH COW 885

Observations on the rectal temperature were made at approximately 15-minute intervals from 5 p. m. to 5.55 p. m. From 5 p. m. to 5.36 p. m. the cow was eating. The cow was up all the time. The results are represented by figure 24.

OBSERVATIONS ON JANUARY 4, 1920, WITH COW 886

Readings of the rectal temperature were made at 15-minute intervals from 5 p. m. to 6 p. m. The cow was not fed till 6 p. m. and was standing all the time. The results are represented by figure 25.

The peculiar feature of the curve is the fall in temperature till 5.30 p. m., followed by a rise from 5.30 p. m. to 6 p. m.

OBSERVATIONS ON MARCH 20, 1920, WITH COW 886

Two readings of the rectal temperature were taken between 5 p. m. to 6.25 p. m. The cow was not fed till 6.25 p. m. and was standing all the time. The results are given in figure 26.

The curve does not show any material change in temperature from 5.15 p. m. to 6.25 p. m.

OBSERVATIONS ON JANUARY 12, 1920, WITH COW 885

Readings of the rectal temperature were taken at approximately 20-minute intervals from 5 p. m. to 6.04 p. m. The cow was not fed till 6 p. m. and was standing all the time. The results are given in figure 27.

OBSERVATIONS ON FEBRUARY 16, 1920, WITH COW 885

Readings of the rectal temperature were taken at half-hour intervals from 5 p. m. to 6 p. m. The cow was not fed till 6 p. m. and was standing all the time. The results are given in figure 28.

The curve shows a fall in temperature from 5 p. m. to 5.30 p. m.

GENERAL CONCLUSIONS WITH REGARD TO THE VARIATIONS IN BODY TEMPERATURE FROM ABOUT 5 P. M. TO ABOUT 7 P. M.

A comparison of the temperature curves obtained when the cow was fed at 5 p. m. with those obtained when the cow was not fed till 6 p. m. shows, in general, that when the cow was fed at 5 p. m. there was a slight rise in temperature till about 5.30 p. m., followed by a slight fall. This rise from 5 p. m. till 5.30 p. m. has been noted in previous observations (fig. 2, 5, 7, 9, 10), when the cows were fed at 5 p. m. When, however, the cow was not fed till 6 p. m., the temperature in most cases not only did not rise from 5 p. m. to 5.30 p. m., but instead dropped slightly. This indicates that eating of the feed raises the body temperature slightly for about ½ hour when the cows receive a maintenance ration.

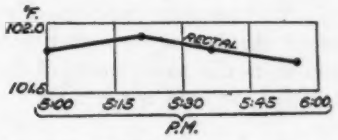


FIG. 24.—Variations in body temperature of cow 885 on January 4, 1920, 5 p. m. to 5.55 p. m. From 5 p. m. to 5.36 p. m. eating; cow standing all the time.

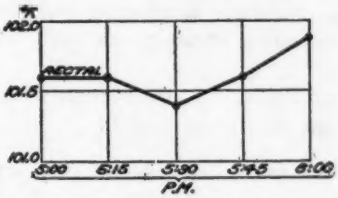


FIG. 25.—Variations in body temperature of cow 886 on January 4, 1920, 5 p. m. to 6 p. m. Cow not fed till 6 p. m.; standing all the time.

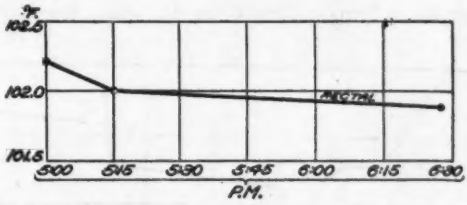


FIG. 26.—Variations in body temperature of cow 886 on March 20, 1920, 5 p. m. to 6.25 p. m. Cow not fed till 6.25 p. m.; standing all the time.

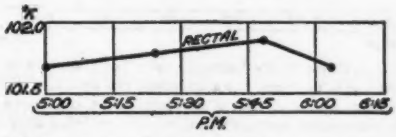


FIG. 27.—Variations in body temperature of cow 885 on January 12, 1920, 5 p. m. to 6.04 p. m. Cow not fed till 6 p. m.; standing all the time.

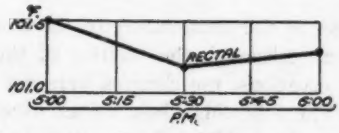


FIG. 28.—Variations in body temperature of cow 885 on February 16, 1920, 5 p. m. to 6 p. m. Cow not fed till 6 p. m.; standing all the time.

The subsequent fall in temperature can be ascribed partly to the fact that the temperature of the feed is lower than that of the body, thus tending to lower somewhat the temperature of the latter, and partly to the natural tendency of the body temperature to drop after a stimulated rise.

The act of defecation did not produce any effect.

The highest rectal temperature obtained during these observations was 102.4° F. (fig. 16), while the lowest was 101.2° (fig. 28). The highest vaginal temperature obtained was 102°, while the lowest was 101.°

The rectal temperature at 6 p. m. fluctuates in all cases, except in one (fig. 28), between 101.5° and 102° F.

OBSERVATIONS ON THE EFFECT OF CHANGE IN POSITION ON BODY TEMPERATURE

It is an established fact that an animal produces more heat when standing than when lying. This being the case, one might, therefore,

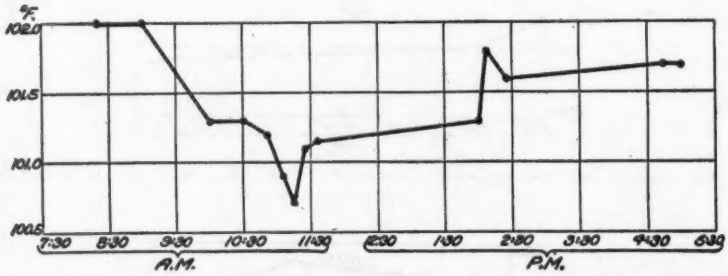


FIG. 29.—Temperature curve of cow 886 for January 5, 1920, 8.20 p. m. to 5 p. m., including effects of change in position. At 8.20 a. m. lying; 8.40 a. m. drank 13.6 kgm. of water at 50° F.; 9 a. m. just lay down; 9 a. m. to 10.30 a. m. lying; 10.31 a. m. forced to get up; 10.50 a. m. immediately before defecating; 10.54 a. m. immediately after defecating; 11.06 a. m. lying since 10.57 a. m.; 11.15 a. m. still lying; 11.24 a. m. up since 11.20 a. m.; 11.36 a. m. still up; 2 p. m. just lay down; 2.02 p. m. forced to get up; 2.06 p. m. up since 2.02 p. m.; 2.24 p. m. down since 2.20 p. m.; 4.45 p. m. down since 4 p. m.; 4.48 p. m. forced to get up; 5 p. m. immediately after defecating.

expect some changes in the temperature of the body when the animal changes its position. Although the position of the animal was noted in the previous observations, the changes were not frequent enough to show any effect. The following observations were made chiefly with the view of studying the possible effects on the body temperature that may arise from a forced or voluntary change in position.

Figure 29 represents observations made on the rectal temperature of cow 886 on January 5, 1920, from 8.20 a. m. to 5 p. m.

The most striking features of the curve are the sudden fluctuations between 10.50 a. m. and 11.24 a. m., and between 2 p. m. and 2.20 p. m. The accelerated fall in temperature (effect of the water) from 10.57 a. m.

to 11.15 a. m. in the former case appear to be due largely to a change from a standing to a lying position, while the subsequent sudden rise at 11.24 a. m. is apparently due largely to the change from a lying to a

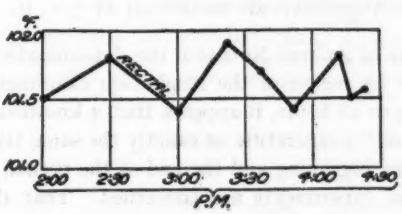


FIG. 30.—Temperature curve of cow 886 for January 13, 1920, 2 p. m. to 4.22 p. m., including effects of change in position. From 2 p. m. to 3.20 p. m. forced to get up; 3.22 p. m. immediately after defecating, urinating with thermometer in rectum; 3.52 p. m. lying since 3.48 p. m.; 4.16 p. m. just got up; 4.22 p. m. still up.

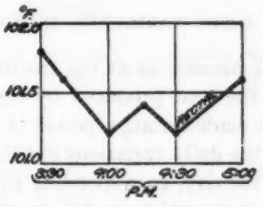


FIG. 31.—Temperature curve of cow 886 for January 15, 1920, 3.30 p. m. to 5 p. m., including effects of change in position. At 3.30 p. m. lying; 3.32 p. m. forced to get up; 3.40 p. m. to 5 p. m. standing; 4.15 p. m. urinated with thermometer in rectum.

standing position. In the second case the sudden rise from 2 p. m. to 2.06 p. m. appears to be due to the change from a lying to a standing position, while the subsequent drop at 2.24 p. m. apparently represents

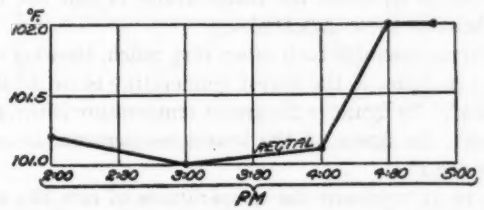


FIG. 32.—Temperature curve of cow 886 on January 30, 1920, 2 p. m. to 4.50 p. m., including effects of change in position. At 2 p. m. lying; 2.43 p. m. to 4.50 p. m. standing.

the effect of the change from the standing to a lying position and also perhaps the tendency for the body temperature to come back to normal. It should be noted that in both cases the effect is not lasting.

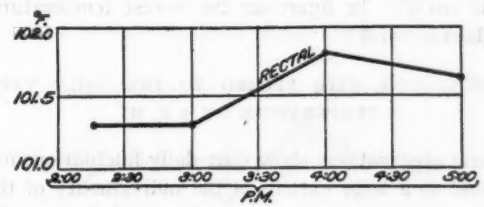


FIG. 33.—Temperature curve of cow 886 on February 16, 1920, 2.15 p. m. to 5 p. m., including effects of position. From 2.15 p. m. to 5 p. m. standing.

A careful study of figures 30 to 35 reveals that, in general, the position of the animal hardly affects the normal course of the fluctuations of its body temperature, for, while the fluctuations were considerable

and rather irregular at the time when the cow did not change her position (fig. 31, 32, 35), the temperature remained fairly uniform when the position was changed (fig. 32 and especially fig. 34).

DAILY VARIATIONS IN BODY TEMPERATURE MEASURED AT 5 P. M.

Inasmuch as at the Institute of Animal Nutrition the determinations of the heat produced by cows by means of the respiration calorimeter are made during a period of 24 or 48 hours, it appears that a knowledge of the daily variations in the body temperature at exactly the same time of the day, corresponding to the beginning and the end of the period, is most essential, as far as those experiments are concerned. That the body temperature of the same animal varies from day to day and from hour to hour has been shown by most of the foregoing observations, even by those made during the time when there was no influence of water or feed (fig. 25–28). To study the extent of the daily fluctuations in body temperature determined at exactly the same time of the day was the object of the next series of observations. To avoid any effect of water drunk or of feed, the observations were made just before feeding at exactly 5 p. m.

Figures 36 to 38 represent the temperatures of cow 886 measured at 5 p. m. for the days there indicated.

All these curves resemble each other very much, showing considerable fluctuations. In figure 36 the lowest temperature is 101.6° F., while the highest is 102.4°. In figure 37 the lowest temperature is 101.4°, while the highest is 102°. In figure 38 the lowest temperature is 101.7°, while the highest is 102.2°.

Figures 39 to 41 represent the temperatures of cow 885 measured at 5 p. m. for the days there indicated.

These three curves resemble each other very much, but they are different from the three preceding curves of cow 886 in that they show much less variation. The lowest temperature in figure 39 is 101.6° F., while the highest is 101.9°. In figure 40 the lowest temperature is 101.8°, while the highest is 101.9°. In figure 41 the lowest temperature is 101.5°, while the highest is 101.8°.

GENERAL CONCLUSIONS WITH REGARD TO THE DAILY VARIATIONS IN TEMPERATURE AT 5 P. M.

The foregoing observations show that daily fluctuations in body temperature depend to a large extent on the individuality of the cow. It is, therefore, not safe to assume in every case that the body temperature of a cow is the same at the same hour of the day, even under normal conditions.

Variations of 0.5° or 0.6° F. in the body temperature of the same animal (886) measured at exactly the same time of the day for several

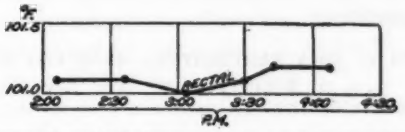


FIG. 34.—Temperature curve of cow 885 for January 13, 1920, 2.06 p. m. to 4.06 p. m., including effects of change in position. At 2.06 p. m. standing; 2.36 p. m. standing; 3.04 p. m. down since 2.48 p. m.; 3.30 p. m. still down; 3.42 p. m. up since 3.38 p. m.; 4.06 p. m. still up.

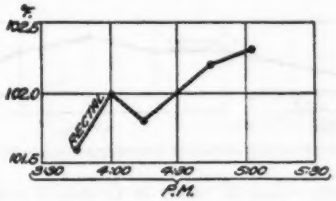


FIG. 35.—Temperature curve of cow 885 for March 22, 1920, 3.45 p. m. to 5.03 p. m., including effects of position. From 3.45 p. m. to 5.03 p. m. standing.

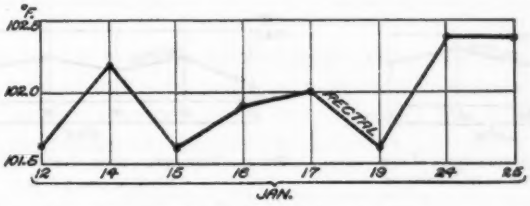


FIG. 36.—Temperature curve of cow 886 for January 12 to January 25, 1920, 5 p. m.

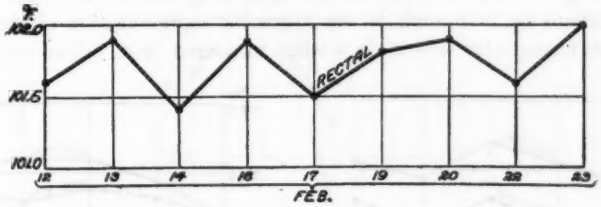


FIG. 37.—Temperature curve of cow 886 for February 12 to February 23, 1920, 5 p. m.

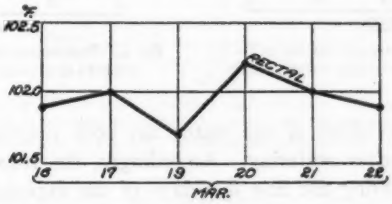


FIG. 38.—Temperature curve of cow 886 for March 16 to March 22, 1920, 5 p. m.

consecutive days are quite common, and greater ones are possible even under identical conditions.

DAILY VARIATIONS IN BODY TEMPERATURE MEASURED AT 8 A. M., 1.30 P. M., AND AT 9 A. M., RESPECTIVELY, FOR SEVERAL CONSECUTIVE DAYS

It has been shown by the very first observations (fig. 1–10) what effect the water drunk under the conditions of the experiment has on

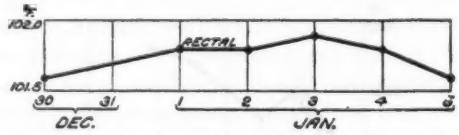


FIG. 39.—Temperature curve of cow 885 for December 30, 1919, to January 5, 1920, 5 p. m.

the body temperature—that if water is drunk in considerable quantity the fall in temperature is very marked, and this effect may last more than three hours, but that after this effect is overcome the temperature

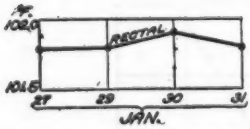


FIG. 40.—Temperature curve of cow 885 for January 27 to January 31, 1920, 5 p. m.

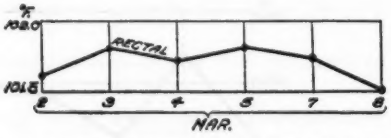


FIG. 41.—Temperature curve of cow 885 for March 2 to March 8, 1920, 5 p. m.

remains quite uniform for about the next three hours. It would therefore perhaps be interesting to see a graphic representation of the temperature changes for several days when measured, first, before watering,

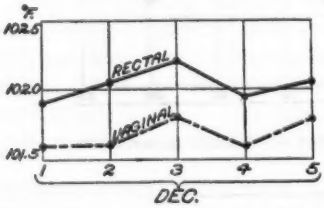


FIG. 42.—Temperature curve of cow 886 for December 1 to December 5, 1919, 8 a. m., before watering.

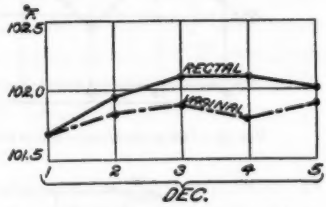


FIG. 43.—Temperature curve of cow 886 for December 1 to December 5, 1919, 1.30 p. m.

second, when the effect of the water has been overcome, and, third, about an hour after watering. Accordingly, the respective temperatures observed during the first few days of the experiment (fig. 1–10), at 8 a. m., at 1.30 p. m., and at 9 a. m., are shown by figures 42 to 46.

Figures 42 and 43 represent the temperatures of cow 886 at 8 a. m. and at 1.30 p. m., respectively, for December 1 to December 5, 1919.

Figures 44 and 45 represent the temperatures of cow 885 at 8 a. m. and at 1.30 p. m., respectively, for December 1 to December 5, 1919. In figure 44 the temperature for December 3 is omitted because the observations did not begin till 8.20 a. m. that day.

On comparing these curves (fig. 42–45) with those obtained at 5 p. m. for the two cows (fig. 36–41) it is observed that while the temperature

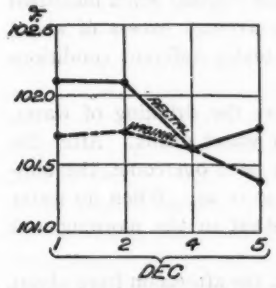


FIG. 44.—Temperature curve of cow 885 for December 1 to December 5, 1919, 8 a. m., before watering.

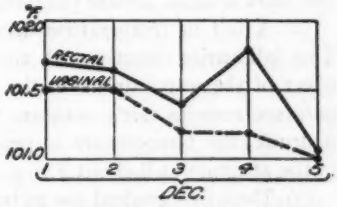


FIG. 45.—Temperature curve of cow 885 for December 1 to December 5, 1919, 1.30 p. m.

of cow 886 at 5 p. m. fluctuated to a large extent from day to day, her body temperature at 8 a. m. or at 1.30 p. m. varied relatively little. On the other hand, the temperature of cow 885, which is very uniform at 5 p. m., varies considerably more at 8 a. m. or at 1.30 p. m. These differ-

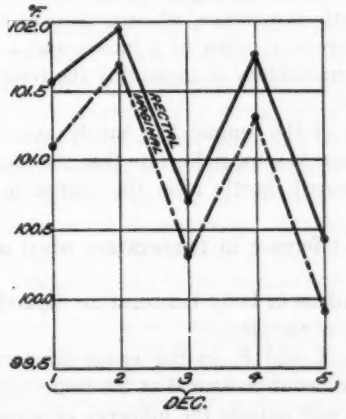


FIG. 46.—Temperature curve of cow 885 for December 1 to December 5, 1919, 9 a. m., showing the effect of water. On December 1 cow drank 29.4 kgm. at 8.30 a. m. On December 2 she refused to drink. On December 3 she drank 22 kgm. at 8.05 a. m. On December 4 she refused to drink. On December 5 she drank 23 kgm. at 8.10 a. m.

ences, apparently due to the individuality of the cow, can not be explained.

Figure 46, representing the temperatures of cow 885 at 9 a. m. for December 1 to December 5, 1919, shows very strikingly the possible

differences in body temperature when measured at exactly the same time of the day but under the influence of the water drunk.

SUMMARY OF RESULTS

The several series of temperature observations on two dry cows lead to the following conclusions:

(1) The rectal temperature is higher than the vaginal when measured at the same depth of 7 inches, showing an average excess of about 0.3° F. The relative values, however, vary under different conditions but show a trend toward parallelism.

(2) A fall in temperature invariably follows the drinking of water. This fall varies directly with the quantity of water drunk. After the effect of the water drunk in the morning has been overcome, the temperature remains fairly constant till about 2.30 p. m. When no water is drunk, the temperature is practically constant in the morning and in the afternoon till about 2.30 p. m.

(3) There is a gradual rise in temperature in the afternoon from about 2.30 p. m. to about 5 p. m.

(4) Eating of feed raises the body temperature slightly for about ½ hour when the cows receive a maintenance ration.

(5) The temperature of the rectum or vagina is decidedly higher when measured as a depth of 6 or 7 inches than at a depth of 4 or 5 inches, thus indicating a temperature gradient.

(6) There is no material change in temperature between a depth of 6 inches and a depth of 7 inches, whereas there is a distinct difference in temperature between a depth of 4 inches and a depth of 6 inches, thus showing the unreliability of measuring the temperature at a depth of less than 6 inches.

(7) The position of the animal has hardly any effect on the body temperature, but there is some indication that the temperature is slightly affected when measured shortly after the change in position has been made (fig. 29).

(8) There is no difference in temperature when measured before or after defecation.

(9) Daily fluctuations in body temperature depend to a great extent on the individuality of the cow.

(10) A variation of 0.8° F. in the rectal temperature of the same animal was observed, when measured at the same time of the day under identical conditions and outside the influence of water or feed (fig. 36), while under the influence of water a difference of 1.3° was observed in two consecutive days measured at the same time of the day (fig. 46).

EFFECT OF TIME OF IRRIGATION ON KERNEL DEVELOPMENT OF BARLEY

By HARRY V. HARLAN, *Agronomist in Charge of Barley Investigations*, and STEPHEN ANTHONY, *formerly Assistant, Office of Cereal Investigations, Bureau of Plant Industry, United States Department of Agriculture*

The studies of kernel development of barley made at Aberdeen, Idaho,[1] in 1915 and 1916, and previously reported,[2] gave such satisfactory results that in 1917 an attempt was made to use this method of inquiry in a study of the effect of irrigation water. It is the common practice in irrigated districts so to arrange the applications of water that the last irrigation is given a considerable time before maturity, usually shortly after flowering. This, of course, is to prevent lodging, for as the weight of the grain increases, the chances of lodging are increased. There is also a widespread belief that during the later stages of ripening little absorption from the soil solution takes place and that the final maturation of the kernel can take place in the shock as well as before cutting. This latter belief was not substantiated in the work of 1915 and 1916, but there seemed to be no definite information as to how late in its growth period the plant could use water or just what occurred when a plant suffered from lack of water.

Although it was hoped that some information could be gained on the general response to applications of water, the effect of delayed irrigation was made the primary object of the experiment. The factors affected by irrigation are so numerous and so involved that the final statement of yield per acre does not afford much basis for interpretation. While the method used may not show any direct relation to yield, it does show the effect on kernel development. The development of the individual kernels is one of the three factors of yield, the other two being the number of kernels per spike and the number of spikes per unit area. The period during which the quantity of water or the application of water affects the size of the kernel is worth determining. Knowledge of the period during which the application of water affects the growth or maturation of the plant affords a basis for the better understanding of irrigation.

[1] These studies were made on the Aberdeen Substation, Aberdeen, Idaho, in connection with cereal experiments conducted cooperatively by the Idaho Agricultural Experiment Station and the Office of Cereal Investigations, Bureau of Plant Industry, United States Department of Agriculture.

[2] HARLAN, Harry V. DAILY DEVELOPMENT OF KERNELS OF HANNCHEN BARLEY FROM FLOWERING TO MATURITY AT ABERDEEN, IDAHO. *In* Jour. Agr. Research, v. 19, no. 9, p. 393-430, 27 fig., pl. 83-91. Literature cited, p. 429. 1920.

——— and ANTHONY, Stephen. DEVELOPMENT OF BARLEY KERNELS IN NORMAL AND CLIPPED SPIKES AND THE LIMITATIONS OF AWNLESS AND HOODED VARIETIES. *In* Jour. Agr. Research, v. 19, no. 9, p. 431-472, 13 fig. 1920.

Journal of Agricultural Research,
Washington, D. C.
xg

Vol. XXI, No. 1
Apr. 1, 1921
Key No. G-221

PLAN OF THE EXPERIMENT

About $\frac{1}{10}$ acre was seeded to Hannchen barley on the Aberdeen Substation, Aberdeen, Idaho. This area was treated as a unit during the early period of growth. It received its last uniform irrigation on June 23. The plot was then subdivided into 16 smaller plots of uniform size. These were inclosed by checks, and each in turn was surrounded by a drainage ditch. Eight of the 16 plots were chosen for the experiment. Plot 1 was handled so as to secure a normal development. It was irrigated on July 10 and July 29. Plot 8 received no water after the uniform irrigation of June 23. Plots 2 to 7, inclusive, received only one application of water after the irrigation of June 23. Water was applied to plot 2 on July 14, to plot 3 on July 17, to plot 4 on July 20, to plot 5 on July 23, to plot 6 on July 26, and to plot 7 on July 29. After the irrigation of July 10, all water was measured, each plot receiving 300 gallons on the dates mentioned, except plot 2, which received only 290 gallons.

Samples were taken on plots 1, 2, and 8 daily from flowering to maturity. Plots 3 to 7, inclusive, were considered to be identical with plot 8 until irrigated. Samples were taken on the day of irrigation either before or soon after the application of water, and daily from that time until maturity. The methods of sampling and of obtaining and recording data have been described previously, and the description will not be repeated here. The results are more than comparable with those reported in the paper on the daily development of the kernels. They are a part of the same data. The data from plot 1 formed the basis of the previous paper. As the data showing daily development have been reported in full for plot 1, all daily data will be omitted here. The summaries in the tables were obtained in the same manner as the summaries previously reported. Slight discrepancies sometimes occur through repeated averages, which do not carry the fraction to sufficient decimal places, and through the fact that a few abnormal kernels are excluded in some cases.

RESULTS

The experimental data recorded are summarized in Table I. The variables recorded were length, lateral diameter, dorsoventral diameter, wet weight, dry weight, water, ash, and nitrogen. All these variables were affected by the time of application of water. The differences are more apparent when considered by variants than when the plot is used as the basis of discussion.

TABLE I.—*Average length, lateral diameter, dorsoventral diameter, and percentage and weight per kernel of dry matter, water, nitrogen, and ash in kernels of Hannchen barley sampled at 24-hour intervals from eight plots variously irrigated at the Aberdeen Substation, Aberdeen, Idaho, in 1917*

PLOT 1

Date.	Length.	Lateral diameter.	Dorsoventral diameter.	Percentage of weight per kernel.				Weight per kernel.				
				Dry matter.	Water.	Nitrogen.[a]	Ash.[a]	Wet weight.	Dry matter.	Water.	Nitrogen.	Ash.
	Mm.	*Mm.*	*Mm.*					*Mgm.*	*Mgm.*	*Mgm.*	*Mgm.*	*Mgm.*
July 15	2.27	1.26	.....	15.9	84.1	3.75	.....	1.9	0.3	1.6	0.01	.....
16	2.88	1.32	0.74	16.0	84.0	4.32	7.91	3.0	.5	2.5	.02	0.05
17	3.93	1.39	.82	19.1	80.9	3.06	7.41	4.5	.9	3.6	.03	.06
18	6.05	1.57	.90	20.1	79.9	.....	6.14	8.0	1.6	6.4	.....	.09
19	7.91	1.79	1.16	22.0	78.0	.....	4.11	12.7	2.8	9.9	.....	.12
20	8.78	1.94	1.30	22.4	77.6	2.27	4.22	15.8	3.5	12.3	.08	.15
21	9.32	2.10	1.48	24.1	75.9	3.14	3.54	19.2	4.6	14.5	.13	.14
22	9.81	2.51	1.71	25.8	74.2	2.33	3.50	25.7	6.6	19.1	.15	.23
23	9.96	2.80	1.90	28.5	71.5	2.07	3.64	31.0	8.8	22.2	.18	.32
24	9.83	2.86	1.90	30.9	69.1	2.13	2.92	32.7	10.1	22.6	.22	.30
25	9.80	3.02	2.05	33.6	66.4	1.94	2.91	36.0	12.1	24.0	.23	.35
26	9.77	3.09	2.06	36.2	63.8	1.96	2.67	38.2	13.9	24.4	.27	.37
27	9.98	3.30	2.25	37.4	62.6	2.03	2.73	44.6	16.6	28.0	.34	.45
28	10.02	3.47	2.33	39.5	60.5	1.98	2.42	48.2	19.0	29.1	.37	.46
29	9.84	3.50	2.42	41.2	58.8	2.03	2.46	49.0	20.2	28.8	.41	.50
30	9.99	3.59	2.50	43.6	56.4	2.01	2.19	53.0	22.8	30.2	.46	.50
31	8.83	3.56	2.54	45.5	54.5	2.12	2.32	52.2	23.7	28.5	.50	.55
Aug. 1	9.10	3.62	2.51	48.1	51.9	1.99	2.26	54.8	26.3	28.4	.52	.59
2	8.87	3.59	2.54	48.7	51.3	1.90	2.03	53.3	25.9	27.4	.49	.52
3	8.87	3.61	2.59	50.3	49.7	1.95	2.05	55.8	28.1	27.8	.55	.58
4	8.96	3.60	2.64	50.8	49.2	2.02	1.97	56.3	28.6	27.7	.58	.56
5	8.66	3.60	2.62	52.9	47.1	1.89	1.94	55.9	29.5	26.4	.56	.57
6	8.78	3.57	2.67	55.1	44.9	2.00	1.89	56.6	31.1	25.5	.62	.59
7	8.77	3.60	2.68	56.4	43.6	2.27	1.93	58.0	32.6	25.4	.75	.63
8	8.53	3.53	2.64	57.2	42.8	2.28	1.88	56.1	32.0	24.1	.76	.60

PLOT 2

July 16	3.2	1.3	0.8	18.1	81.9	3.15	.....	3.4	0.6	2.8	0.02	.....
17	3.4	1.4	.9	18.9	81.1	2.63	4.88	4.3	.8	3.5	.02	0.05
18	5.6	1.5	.9	19.9	80.1	2.43	6.33	7.0	1.4	5.6	.03	.09
19	6.6	1.7	1.0	21.3	78.7	2.11	5.62	8.8	1.9	6.9	.04	.12
20	7.9	1.8	1.2	22.1	77.9	2.26	4.91	13.0	2.9	10.1	.07	.13
21	9.0	2.0	1.4	23.5	76.5	2.17	.....	17.5	4.1	13.4	.09	.....
22	9.6	2.4	1.7	25.6	74.4	2.38	3.48	24.1	6.2	17.9	.11	.27
23	9.4	2.6	1.8	27.8	72.2	4.33	3.79	26.9	7.5	19.4	.35	.26
24	9.7	2.8	1.9	29.8	70.2	2.28	.....	31.5	9.4	22.1	.21	.....
25	9.5	2.8	1.9	32.4	67.6	2.14	.....	31.1	10.1	21.0	.22	.....
26	9.9	3.0	2.0	34.0	66.0	1.97	.....	36.3	12.3	24.0	.24	.....
27	9.7	3.3	2.1	36.7	63.3	2.16	.....	40.6	14.9	25.7	.32	.....
28	9.8	3.3	2.2	36.3	63.7	2.32	.....	42.5	15.4	27.1	.36	.....
29	9.7	3.3	2.3	40.4	59.6	2.27	.....	42.5	17.1	25.4	.39	.....
30	9.8	3.5	2.3	42.3	57.7	2.02	.....	46.7	19.7	27.0	.40	.....
31	8.6	3.4	2.4	45.8	54.2	2.11	.....	48.3	22.2	26.1	.46	.....
Aug. 1	8.8	3.4	2.4	45.9	54.1	2.16	.....	47.7	21.9	25.8	.47	.....
2	8.7	3.5	2.5	47.2	52.8	2.22	.....	51.9	24.5	27.4	.54	.....
3	8.7	3.4	2.3	50.2	49.8	2.41	.....	45.9	23.0	22.9	.55	.....
4	8.5	3.5	2.4	50.7	49.3	2.56	.....	47.5	23.8	23.7	.61	.....
5	8.7	3.5	2.6	51.5	48.5	2.30	.....	52.2	26.9	25.3	.62	.....
6	8.3	3.2	2.3	57.0	43.0	2.39	.....	44.3	25.2	19.1	.60	.....
7	8.3	3.3	2.3	59.9	40.1	2.36	.....	45.4	26.6	18.8	.63	.....
8	8.6	3.4	2.5	60.2	39.8	2.54	.....	49.7	29.8	19.9	.76	.....
9	8.3	3.2	2.4	91.8	8.2	1.74	.....	43.2	39.6	3.6	.69	.....

[a] On dry-matter basis.

TABLE I.—*Average length, lateral diameter, dorsoventral diameter, and percentage and weight per kernel of dry matter, water, nitrogen, and ash in kernels of Hannchen barley sampled at 24-hour intervals from eight plots variously irrigated at the Aberdeen Substation, Aberdeen, Idaho, in 1917*—Continued

PLOT 3

Date.	Length.	Lateral diameter.	Dorsoventral diameter.	Percentage of weight per kernel.				Weight per kernel.				
				Dry matter.	Water.	Nitrogen.[a]	Ash.[a]	Wet weight.	Dry matter.	Water.	Nitrogen.	Ash.
	Mm.	*Mm.*	*Mm.*					*Mgm.*	*Mgm.*	*Mgm.*	*Mgm.*	*Mgm.*
July 17	4.3	1.5	0.9	21.3	78.7	3.41	5.90	5.2	1.1	4.1	0.04	0.06
18	6.1	1.6	.9	21.6	78.4	2.37	4.00	8.2	1.8	6.4	.04	.07
19	7.3	1.7	1.1	22.5	77.5	2.44	3.80	10.9	2.5	8.4	.06	.08
20	8.4	2.0	1.3	23.3	76.7	2.24	3.37	15.9	3.7	12.2	.09	.11
21	9.1	2.2	1.5	23.9	76.1	2.18	4.67	18.9	4.5	14.4	.09	.24
22	9.8	2.5	1.6	25.9	74.1	2.56	3.61	24.1	6.3	17.8	.15	.25
23	9.3	2.5	1.7	26.8	73.2	2.14	3.87	26.4	7.1	19.3	.17	.25
24	9.8	3.0	2.0	31.5	68.5	2.24	3.79	35.3	11.2	24.1	.28	.38
25	9.8	3.1	2.0	31.2	68.8	2.06	4.02	35.5	11.0	24.5	.23	.43
26	9.9	3.2	2.1	35.3	64.7	.....	3.17	38.9	13.7	25.2	.....	.43
27	9.8	3.3	2.2	37.6	62.4	2.07	2.20	44.1	16.6	27.5	.35	.36
28	9.7	3.4	2.3	36.4	63.6	2.04	2.60	45.9	16.7	29.2	.34	.43
29	9.6	3.5	2.3	40.8	59.2	2.00	2.30	45.8	18.7	27.1	.39	.41
30	9.1	3.6	2.5	41.0	59.0	2.00	.....	51.7	21.6	30.1	.45	.....
31	8.9	3.6	2.5	41.8	58.2	1.96	2.14	52.7	22.0	30.7	.42	.48
Aug. 1	8.8	3.6	2.5	43.6	56.4	2.07	2.08	53.2	23.1	30.1	.46	.50
2	8.7	3.6	2.6	48.1	51.9	2.23	2.06	53.8	25.8	28.0	.58	.53
3	8.7	3.6	2.6	49.1	50.9	2.41	2.17	56.0	27.5	28.5	.67	.59
4	8.8	3.7	2.7	49.1	50.9	2.11	2.14	57.5	28.2	29.3	.61	.59
5	8.6	3.6	2.6	53.0	47.0	2.17	1.93	56.3	29.8	26.5	.64	.58
6	8.6	3.6	2.6	55.3	44.7	2.13	2.04	55.5	30.6	24.9	.65	.63
7	8.4	3.5	2.5	56.8	43.2	2.36	1.96	53.7	30.4	23.3	.70	.62
8	8.2	3.4	2.5	56.3	43.7	2.55	1.71	51.1	28.8	22.3	.64	.55

PLOT 4

July 20	8.6	1.9	1.3	24.4	75.6	2.77	3.9	15.5	3.8	11.7	0.10	0.15
21	8.9	2.0	1.3	24.3	75.7	3.08	4.8	16.1	3.9	12.2	.12	.19
22	9.7	2.5	1.6	27.2	72.8	2.71	3.6	23.6	6.4	17.2	.20	.20
23	9.7	2.8	1.8	28.3	71.7	2.65	3.2	27.9	7.9	20.0	.20	.27
24	9.5	2.9	1.9	29.5	70.5	2.38	3.3	31.8	9.4	22.4	.24	.28
25	9.9	3.1	2.1	33.3	66.7	1.15	3.8	37.9	12.6	25.3	.14	.49
26	9.8	3.2	2.1	34.2	65.8	2.11	3.2	34.4	13.5	20.9	.27	.45
27	9.7	3.4	2.2	34.3	65.7	2.39	3.0	41.3	14.1	27.2	.34	.42
28	9.9	3.4	2.3	36.1	63.9	2.19	2.9	44.3	16.0	28.3	.34	.48
29	9.9	3.4	2.3	39.9	60.1	1.39	3.2	46.1	18.6	27.5	.26	.....
30	8.8	3.5	2.4	42.2	57.8	2.12	2.3	47.1	19.8	27.3	.42	.46
31	9.0	3.6	2.5	42.8	57.2	2.25	2.4	52.6	22.5	30.1	.53	.51
Aug. 1	8.8	3.6	2.5	46.2	53.8	2.31	2.0	52.2	24.1	28.1	.55	.48
2	9.0	3.7	2.6	46.9	53.1	2.31	2.3	58.2	27.3	30.9	.63	.63
3	8.7	3.7	2.6	49.8	50.2	2.43	2.0	56.3	28.0	28.3	.69	.55
4	8.6	3.5	2.6	50.0	50.0	2.35	2.2	52.7	26.4	26.3	.59	.60
5	8.7	3.6	2.7	51.8	48.2	2.62	2.0	54.8	28.4	26.4	.73	.58
6	8.5	3.6	2.6	53.7	46.3	2.90	2.3	54.1	29.1	25.0	.75	.73
7	8.6	3.6	2.6	55.7	44.3	1.83	2.0	54.7	30.5	24.2	.56	.61
8	8.3	3.5	2.5	58.1	41.9	2.75	1.7	50.6	29.4	21.2	.81	.50

PLOT 5

July 23	9.5	2.9	1.8	32.1	67.9	1.96	3.3	29.9	9.6	20.3	0.18	0.33
24	9.7	2.9	1.8	31.0	69.0	2.87	2.8	30.2	9.4	20.8	.26	.27
25	9.7	3.2	2.1	34.6	65.4	2.31	2.1	37.4	13.0	24.4	.26	.31
26	9.6	3.1	1.9	33.3	66.7	2.63	2.1	34.8	11.6	23.2	.27	.28
27	9.7	3.3	2.1	35.1	64.9	2.55	3.2	40.1	14.1	26.0	.39	.41
28	9.7	3.4	2.2	36.8	63.2	2.82	.....	43.3	15.9	27.4	.42	.....
29	9.5	3.4	2.2	41.4	58.6	.....	2.2	44.6	18.5	26.1	.....	.40
30	8.8	3.5	2.4	43.8	56.2	2.62	2.4	48.8	21.4	27.4	.52	.55
31	8.7	3.4	2.4	44.1	55.9	2.13	2.1	48.0	21.1	26.9	.43	.47
Aug. 1	8.8	3.5	2.4	44.5	55.5	1.96	2.3	50.6	22.5	28.1	.41	.55
2	8.4	3.5	2.5	48.5	51.5	2.28	2.2	49.6	24.1	25.5	.54	.54
3	8.4	3.6	2.4	47.8	52.2	2.84	2.1	48.5	23.2	25.3	.63	.51
4	8.6	3.5	2.5	48.9	51.1	2.58	2.1	51.6	25.2	26.4	.67	.52
5	8.3	3.6	2.5	51.7	48.3	2.56	2.2	51.8	26.8	25.0	.66	.61
6	8.6	3.5	2.6	52.2	47.8	2.88	1.7	51.9	27.0	24.9	.78	.46
7	8.4	3.5	2.5	56.1	43.9	2.88	2.5	53.4	29.9	23.5	.85	.76
8	8.1	3.4	2.6	54.9	45.1	2.52	1.9	50.0	27.5	22.5	.73	.50
9	8.1	3.4	2.5	54.7	45.3	2.99	1.9	50.6	27.7	22.9	.90	.48

[a] On dry-matter basis.

TABLE I.—*Average length, lateral diameter, dorsoventral diameter, and percentage and weight per kernel of dry matter, water, nitrogen, and ash in kernels of Hannchen barley sampled at 24-hour intervals from eight plots variously irrigated at the Aberdeen Substation, Aberdeen, Idaho, in 1917*—Continued

PLOT 6

Date.	Length.	Lateral diameter.	Dorsoventral diameter.	Percentage of weight per kernel.				Weight per kernel.				
				Dry matter.	Water.	Nitrogen.[a]	Ash.[a]	Wet weight.	Dry matter.	Water.	Nitrogen.	Ash.
	Mm.	*Mm.*	*Mm.*					*Mgm.*	*Mgm.*	*Mgm.*	*Mgm.*	*Mgm.*
July 26	9.4	3.0	1.8	37.5	62.5	2.81	2.2	32.4	12.2	20.2	0.25	0.26
27	9.8	3.3	2.1	38.9	61.1	2.21	2.2	41.1	16.0	25.1	.34	.36
28	9.8	3.3	2.2	39.2	60.8	2.22	2.1	42.7	16.7	26.0	.37	.35
29	9.7	3.3	2.2	40.2	59.8	2.68	1.9	40.7	16.3	24.4	.44	.31
30	9.0	3.5	2.3	41.7	58.3	2.37	1.9	46.8	19.5	27.3	.45	.38
31	8.8	3.4	2.3	37.4	62.6	3.79	2.4	44.9	16.8	28.1	.50	.49
Aug. 1	8.6	3.3	2.2	47.5	52.5	2.27	1.9	42.0	20.0	22.0	.47	.36
2	8.6	3.4	2.4	49.1	50.9	2.45	1.9	51.1	25.1	26.0	.59	.30
3	8.3	3.4	2.3	49.8	50.2	2.88	1.6	44.1	22.0	22.1	.58	.38
4	8.5	3.4	2.4	49.0	51.0	2.39	2.1	46.7	22.9	23.8	.61	.63
5	9.0	3.6	2.6	51.8	48.2	2.83	2.2	55.9	28.9	27.0	.74	.70
6	8.4	3.4	2.4	51.9	48.1	2.38	2.6	47.3	24.6	22.7	.65	.57
7	8.3	3.4	2.4	55.1	44.9	2.79	1.6	48.0	26.4	21.6	.78	.40
8	8.4	3.4	2.5	55.4	44.6	.....	1.7	48.2	26.7	21.5	.....	.46

PLOT 7

July 29	9.3	3.2	2.0	43.6	56.4	3.04	2.0	37.8	16.5	21.3	0.51	0.32
30	8.8	3.3	2.2	46.1	53.9	2.37	2.1	49.1	19.4	22.7	.45	.42
31	8.6	3.4	2.4	46.6	53.4	2.43	1.8	45.6	21.2	24.4	.52	.38
Aug. 1	8.8	3.3	2.2	47.9	52.1	2.63	2.1	44.6	21.3	23.3	.57	.44
2	8.6	3.3	2.3	48.0	52.0	3.01	1.9	42.5	20.4	22.1	.62	.39
3	8.5	3.3	2.3	50.6	49.4	.....	1.7	43.8	22.9	20.9	.....	.39
4	8.7	3.4	2.3	50.1	49.9	2.77	1.7	45.3	22.7	22.6	.59	.41
5	8.5	3.4	2.3	51.1	48.9	2.61	1.7	46.0	23.5	22.5	.66	.37
6	8.3	3.2	2.3	53.1	46.9	2.81	2.2	42.2	22.4	19.8	.62	.50
7	8.2	3.2	2.3	55.2	44.8	2.55	2.2	44.1	24.4	19.7	.68	.49
8	8.1	3.2	2.4	57.3	42.7	2.53	1.6	45.7	26.1	19.6	.66	.42

PLOT 8

July 16	3.7	1.4	0.9	22.2	77.8	2.74	9.6	4.0	0.9	3.1	0.02	0.09
17	4.7	1.5	.8	22.0	78.0	2.40	4.4	5.9	1.3	4.6	.03	.07
18	6.0	1.6	.9	22.2	77.8	2.36	6.8	7.3	1.6	5.7	.03	.14
19	8.0	1.8	1.1	23.7	76.3	2.05	4.5	14.0	3.3	10.7	.07	.13
20	8.6	2.0	1.3	24.6	75.4	2.40	3.8	15.7	3.9	11.8	.09	.16
21	9.5	2.1	1.5	25.3	74.7	1.87	3.2	19.5	4.9	14.6	.09	.16
22	9.6	2.3	1.6	26.6	73.4	2.62	3.5	22.6	6.0	16.6	.16	.21
23	9.6	2.5	1.8	29.9	70.1	2.35	3.1	27.2	8.1	19.1	.20	.24
24	9.6	3.0	1.9	34.9	65.1	2.37	2.2	33.4	11.7	21.7	.29	.24
25	9.7	2.9	1.9	36.2	63.8	2.10	3.0	34.9	12.7	22.2	.31	.33
26	9.8	3.1	2.0	38.8	61.2	2.19	2.5	37.0	14.4	22.6	.33	.36
27	9.7	3.2	2.1	39.4	60.6	2.32	2.3	40.6	16.0	24.6	.35	.38
28	9.7	3.2	2.0	40.8	59.2	2.84	2.6	37.9	15.5	22.4	.41	.41
29	9.8	3.3	2.1	44.2	55.8	2.41	2.3	40.4	17.9	22.5	.44	.40
30	8.8	3.3	2.2	46.7	53.3	2.85	2.5	42.3	19.8	22.5	.56	.49
31	8.8	3.4	2.2	46.8	53.2	2.49	2.2	43.9	20.5	23.4	.51	.45
Aug. 1	8.5	3.3	2.2	48.9	51.1	2.91	2.1	41.4	20.2	21.2	.62	.40
2	8.4	3.2	2.3	50.9	49.1	2.56	2.0	43.5	22.1	21.4	.59	.43
3	8.6	3.2	2.2	53.1	46.9	2.86	1.9	42.4	22.4	20.0	.68	.40
4	8.4	3.2	2.2	54.0	46.0	2.86	1.6	41.6	22.4	19.2	.65	.35
5	8.4	3.0	2.1	62.6	37.4	2.69	1.9	34.6	21.6	13.0	.61	.39
6	8.3	2.9	2.0	64.2	35.8	3.16	2.0	33.0	21.2	11.8	.67	.42

[a] On dry-matter basis.

The length of kernel is not a very satisfactory index of development. As has been previously shown, the full length is attained within a few days after flowering and remains nearly constant during the remainder of the period of development. As the grain ripens, however, the loss

of water and consequent turgor result in a slight decrease in length. The average lengths of kernels from the 8 plots are shown in figure 1. These are averages of daily measurements until July 23. After that date they are the averages of two days, as the length had become so nearly constant as to make daily averages of no advantage. The drop in length on July 30 is due to a change in the method of measurement.

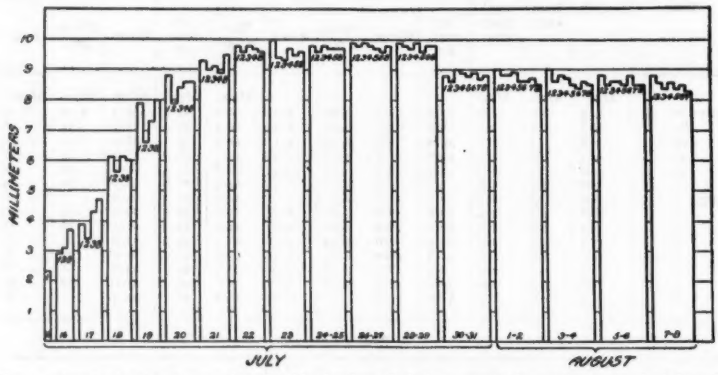


FIG. 1.—Graph showing average length of barley kernels during growth, from plots variously irrigated.

After this date it was possible to measure the kernels without including the ovary tissues, which had then been largely resorbed. Previous to this date the measurements include ovary tissue about 1 mm. in length.

Figure 1 shows two things. Plot 1, which, because of the irrigation designed to maintain satisfactory growth, exceeded the other plots in size of kernels, possessed no advantage at the beginning. Its kernels

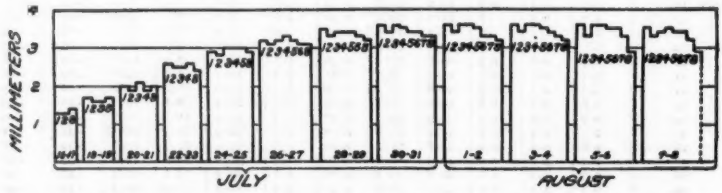


FIG. 2.—Graph showing average lateral diameter of barley kernels during growth, from plots variously irrigated.

were of no greater size than those of the other plots. On the other hand, it is apparent that the kernels from plots 7 and 8 never attained the length of the kernels from plot 1 and that the shrinking at maturity occurred earlier in these plots.

The maximum lateral diameter of the kernel was not attained until the last of July. As maturity approached, there was slight decrease. In figure 2 the lateral measurements of kernels from plot 2 are shown to

be considerably lower than those of kernels from plot 3 or 4. A part of this may be due to soil conditions, but a part is due also to the greater culm formation. The irrigation of July 14 on plot 2 stimulated stooling to such an extent that more spikes were produced in this plot than in any of those irrigated later. As it received no further irrigation, the competition was more intense and the plants suffered from drouth toward maturity. As maturity approached, the diameters of kernels from plots 6 and 7 were greater than those of kernels from plot 8, showing benefit from late irrigation.

The dorsoventral diameter (fig. 3) does not reach its maximum until just before maturity. There was little difference between these measurements of kernels from the different plots until July 27. After this date there is an evident relation between the dorsoventral diameter and the date of the application of water, excepting in plot 2, which was somewhat abnormal. The kernels from plots 3 and 4 are almost equal to those of plot 1. These kernels, it will be remembered, are from selected

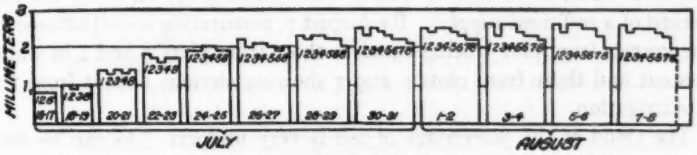


FIG. 3.—Graph showing dorsoventral diameters of barley kernels during growth, from plots variously irrigated.

spikes, the total number of spikes being much less in those plots. The plants in plots 6 and 7 were able to use the water applied as late as July 26 and 29. They showed an increase in the dorsoventral diameter of the kernels as compared with those from plot 8, and the maturation was delayed by the application.

The average weights per kernel of all intermediate plots fell between those of plot 1 and plot 8. The data on weights present one surprising feature. The wet weight per kernel is an earlier index of final size of kernel than is the dry weight. In figures 4 to 10 it appears that the moisture of the irrigation of June 23 was sufficient to maintain a maximum growth on plot 8 until July 27. After that date, the wet weight of kernels from plot 8 was less than that of those from plots 1 to 4. In figures 11 to 17 it will be seen that this is not the case with the dry matter. The weight of dry matter in kernels from plot 8 is equal to that of those from plots 2, 3, and 4 until July 30. The cause of this is not evident. It would appear that the size of kernel is determined before the rate of deposit of material is checked. In figure 18, the water content of the kernels from plot 8 is seen to have reached the maximum by July 27. This is not true in any other plot. This means that whatever change takes

place at this time occurs under the conditions of plot 8 two or three days earlier than in plots 1 to 4. This change may mark the end of the addition of new cells, the abandonment of the central cells for active deposition, the entering of the second stage of starch formation where numerous new grains are started, or it may be some fundamental change the significance of which is not yet recognized.

The kernels from plots 5, 6, and 7 show departure from the rate of deposit in those of plot 8 at later dates. There is a departure in all cases; and even in plot 7, irrigated as late as July 29, the kernels are significantly greater in size and their maturation date is postponed by the irrigation.

The status of the water supply on succeeding days is more apparent in figure 18. The course of the water content of kernels from plot 1 is here seen to be very regular. From this plot four samples were taken instead of two, and the more favorable irrigation caused a more uniform development in the plants. If some allowance is made for plot 2, the effect of time of irrigation is quite apparent. By August 1, plot 2 has begun to suffer from lack of water, while 3 and 4 are enjoying the full benefit of a sufficient supply. By August 7, maturation is well advanced, the kernels from plot 5 being equal to those from plots 3 and 4 in water content and those from plots 6 and 7 showing obvious benefit from the late irrigation.

The trend of the percentage of ash is very uniform. As can be seen from the table, there is a gradual daily decrease from about 8 per cent at flowering to less than 1 per cent at maturity. When expressed in milligrams per kernel, the ash content bears a direct though not exact relationship to quantity of the water used. This is apparent in figure 19, where the ash per kernel is averaged in 3-day periods. There is some evidence that the application of water retards the deposit of ash for two or three days following irrigation. The curves of July 31 and August 6 are strongly suggestive of the availability of water. It is to be supposed that plots 2 to 4 would use more water than those irrigated later, as they had the use of water for a longer period. Plots 3 and 4 received much less water than plot 1, but they contained fewer culms and the water per culm seems to have been sufficient for an equal deposit of ash.

The nitrogen determinations were not satisfactory. As may be seen in the table, the percentages varied from day to day more than seems natural. At first this is due to extremely small samples, but the variation is just as great at maturity. No definite conclusions can be drawn, but from figure 20 it appears that a plentiful water supply may hinder the deposit of nitrogen. As much nitrogen apparently is deposited in the kernels in plots suffering for water as in those amply provided with it. Of course the percentage of nitrogen is higher in the smaller kernels.

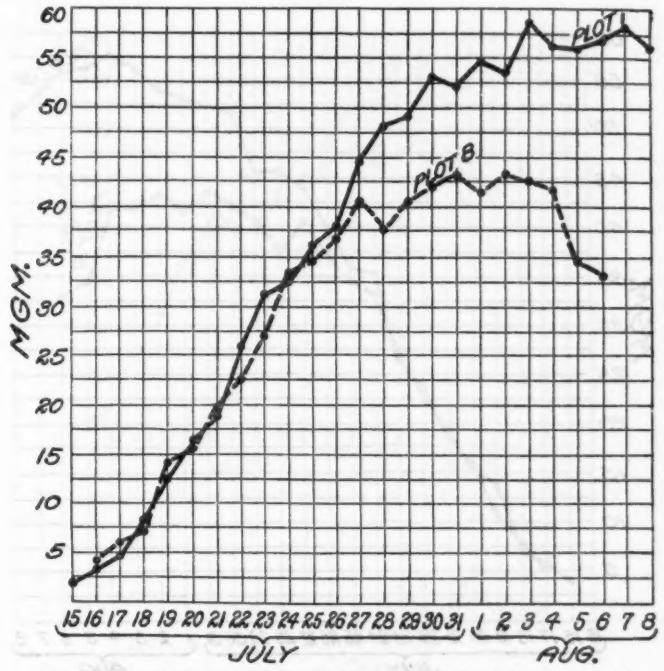


FIG. 4.—Graph showing wet weight in milligrams of barley kernels from plots 1 and 8.

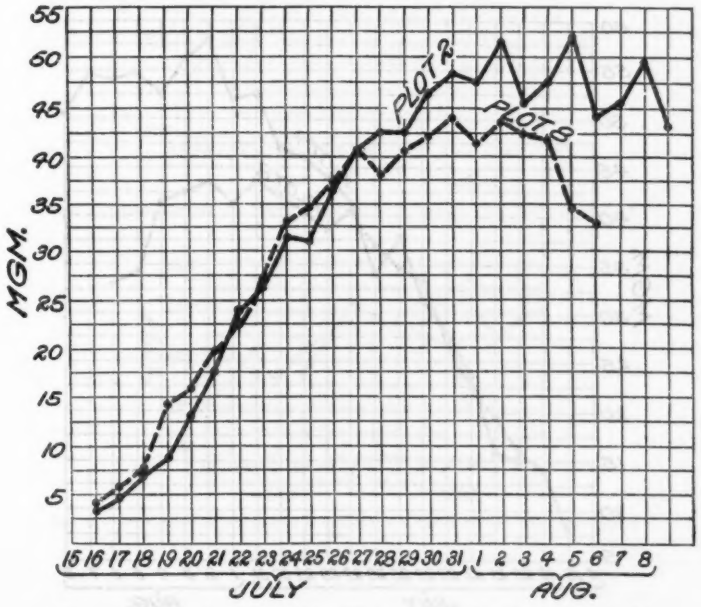


FIG. 5.—Graph showing wet weight in milligrams of barley kernels from plots 2 and 8.

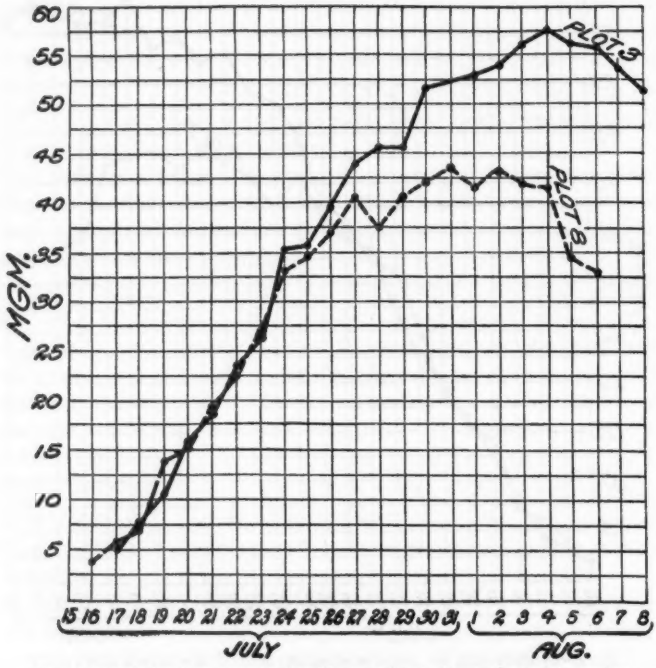


FIG. 6.—Graph showing wet weight in milligrams of barley kernels from plots 3 and 8.

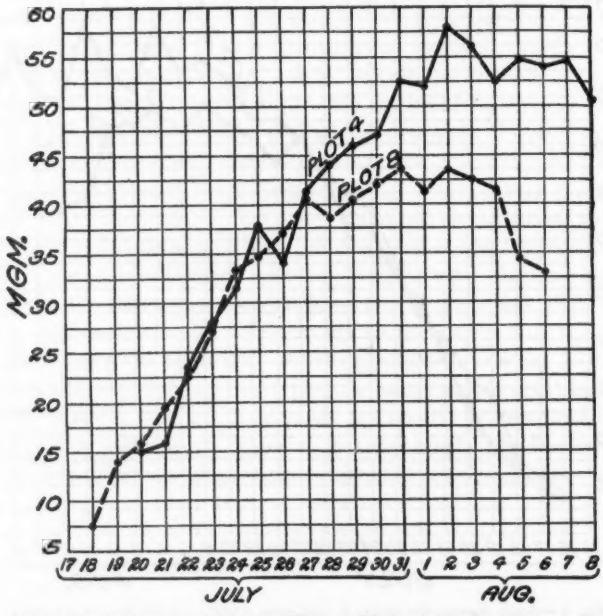


FIG. 7.—Graph showing wet weight in milligrams of barley kernels from plots 4 and 8.

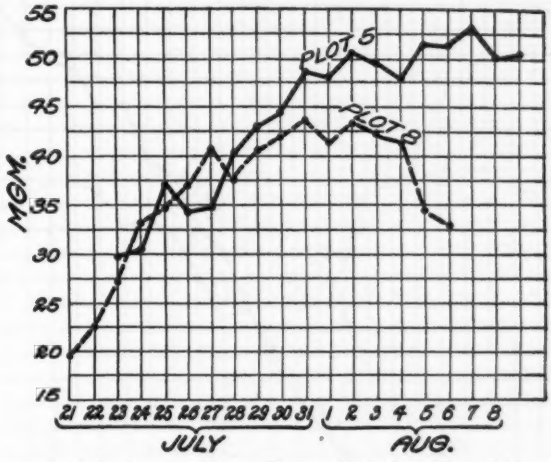


FIG. 8.—Graph showing wet weight in milligrams of barley kernels from plots 5 and 8.

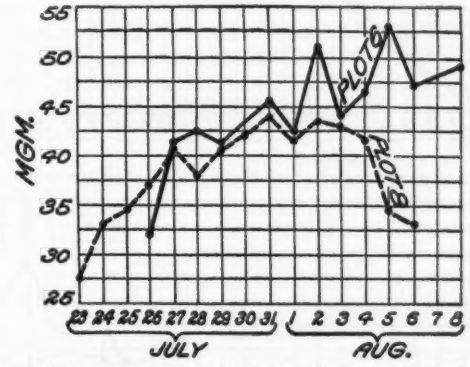


FIG. 9.—Graph showing wet weight in milligrams of barley kernels from plots 6 and 8.

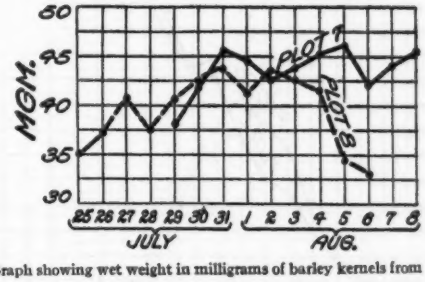


FIG. 10.—Graph showing wet weight in milligrams of barley kernels from plots 7 and 8.

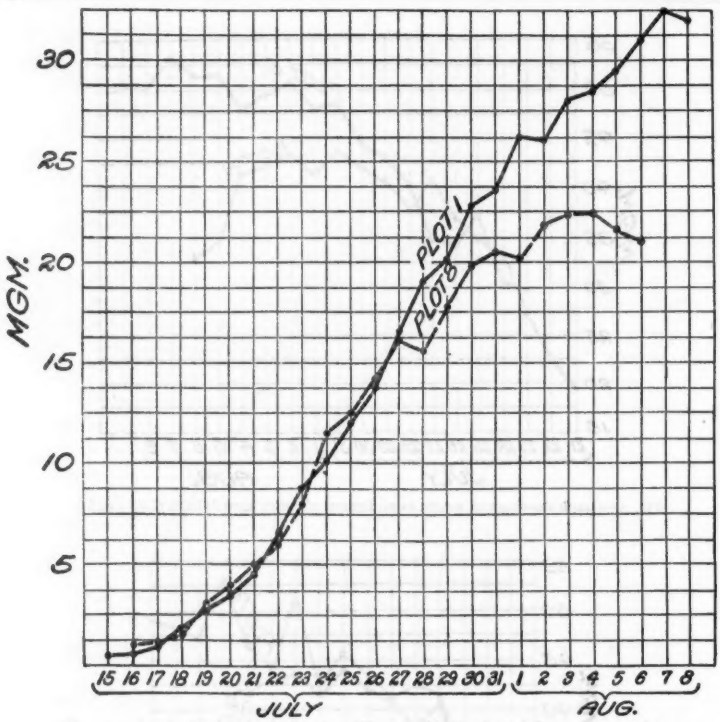


FIG. 11.—Graph showing dry weight in milligrams of barley kernels from plots 1 and 8.

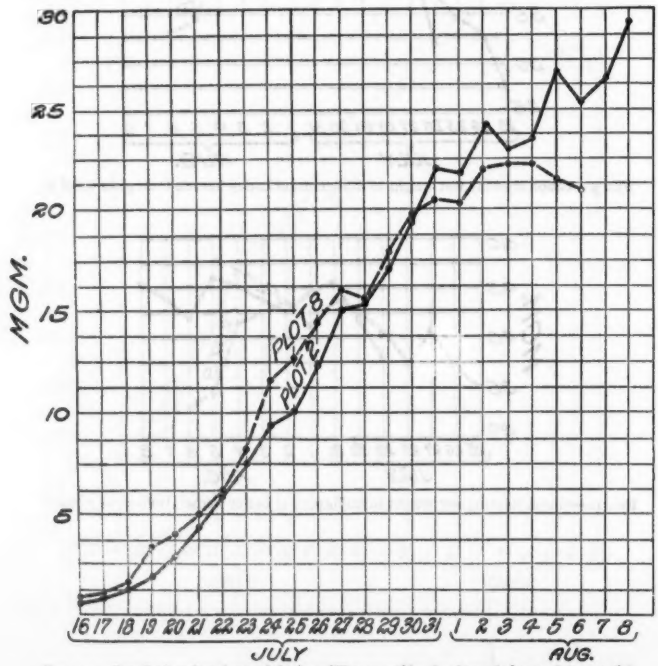


FIG. 12.—Graph showing dry weight in milligrams of barley kernels from plots 2 and 8.

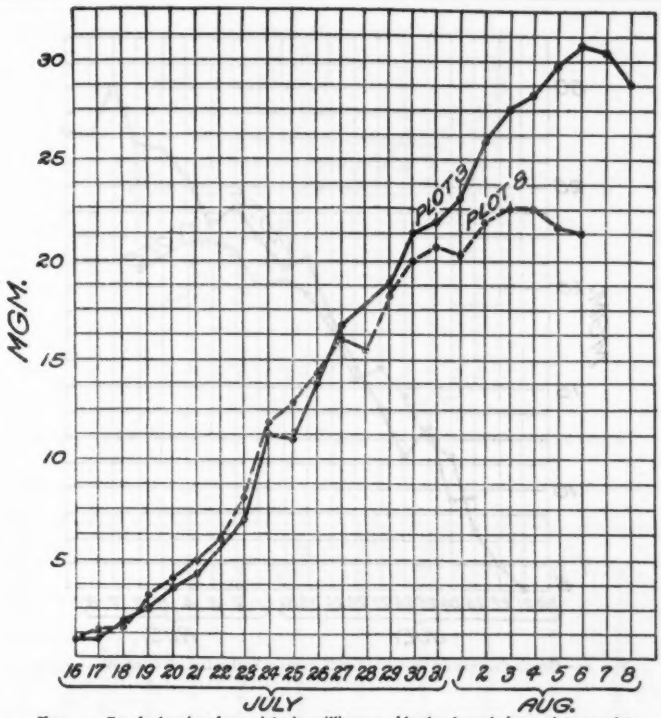


FIG. 13.—Graph showing dry weight in milligrams of barley kernels from plots 3 and 8.

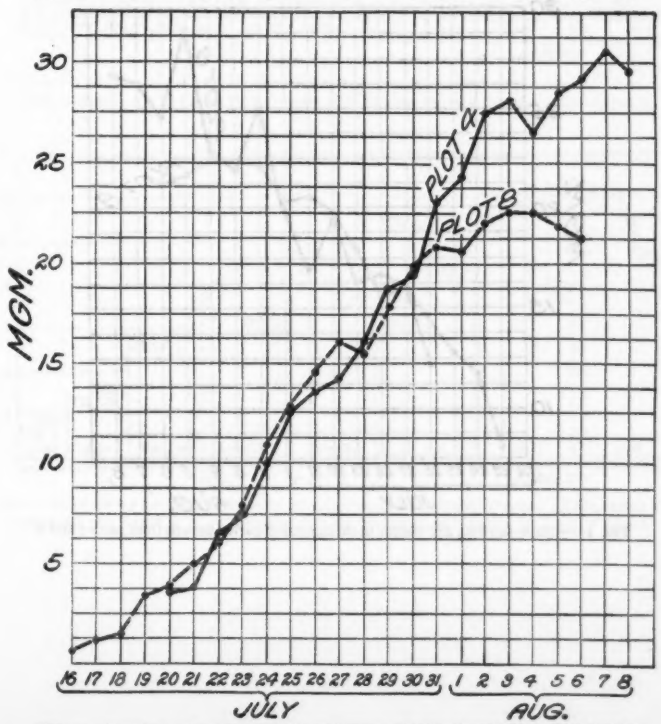


FIG. 14.—Graph showing dry weight in milligrams of barley kernels from plots 4 and 8.

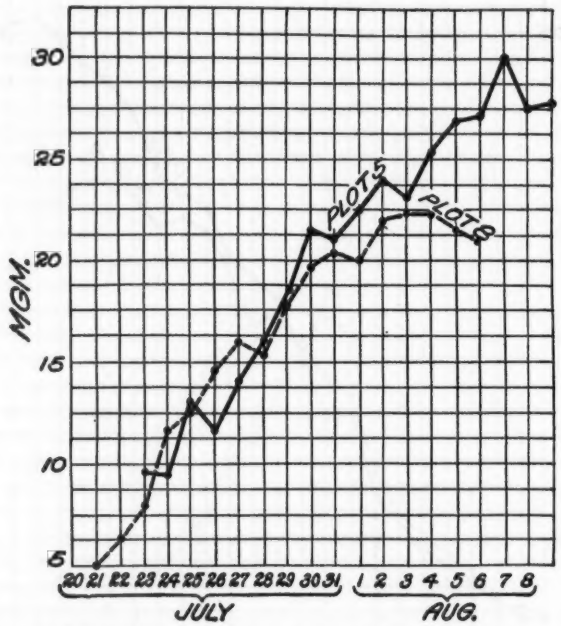


FIG. 15.—Graph showing dry weight in milligrams of barley kernels from plots 5 and 8.

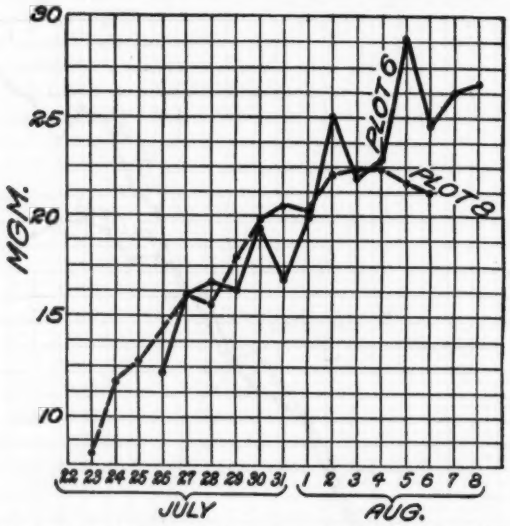


FIG. 16.—Graph showing dry weight in milligrams of barley kernels from plots 6 and 8.

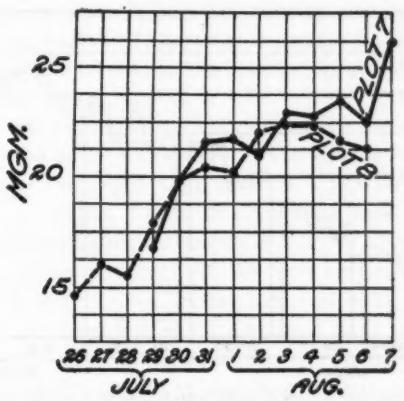


FIG. 17.—Graph showing dry weight in milligrams of barley kernels from plots 7 and 8.

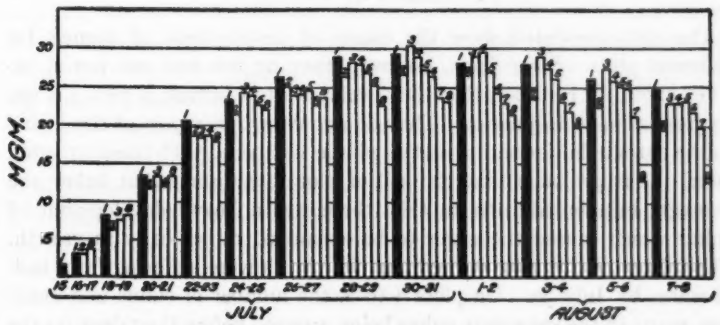


FIG. 18.—Graph showing water content of barley kernels from plots variously irrigated. Data shown are in milligrams per kernel and are averages of daily measurements during each 2-day period.

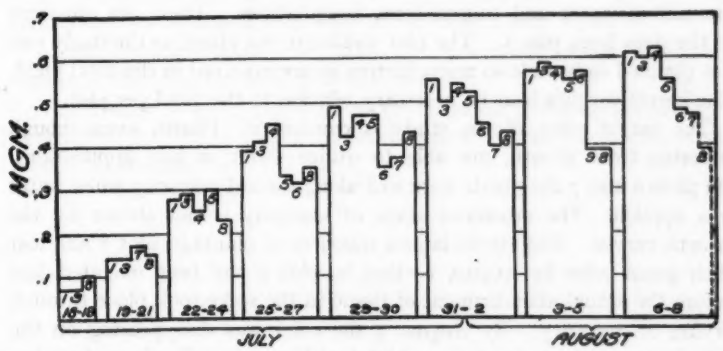


FIG. 19.—Graph showing ash content in barley kernels from plots variously irrigated. Data shown are in milligrams per kernel and are averages of daily measurements during each 3-day period.

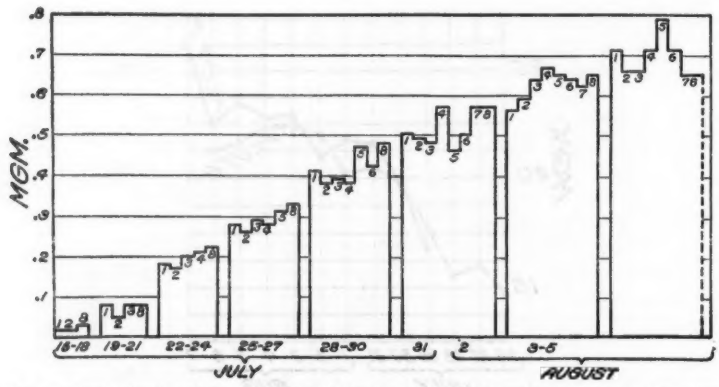


FIG. 20.—Graph showing nitrogen content of barley kernels from plots variously irrigated. Data shown are in milligrams per kernel and are averages of daily measurements during each 3-day period.

DISCUSSION OF RESULTS

The data presented show the course of development of kernels for different plots. Some facts, however, they do not and can not show. They show, for instance, that the development of kernels in plot 2 is not so great as in plots 3 and 4. They do not show that a part of this is due to the extra culm formation on this plot as compared with those irrigated later. It is probable that the soil of plot 2 was somewhat below the average; but, in addition to this, there was a heavy development of culms which caused the water to be exhausted rather early in growth. The foliage of this plot showed that its plants were suffering from lack of water by July 30. On plots 3 to 8, the number of culms was much less, many of the secondary culms being arrested before they drew on the water supply. On the plots irrigated late in the series, wolf plants developed which by their extra development used more than an average amount of water and caused some irregularities. These are apparent in the data from plot 5. The plot yields are not given, as the study was not planned to include so many factors as are involved in the total yield. The kernel weights bear no necessary relation to the yield per plot.

The major point of the study is conclusive. Plants, even though suffering from drouth, are able to utilize water in late applications. On plots 6 and 7 the plants were well along toward maturity when water was applied. The advanced stage of maturity is not shown by the growth curves. The sterile lateral spikelets of plants in plot 8 had lost their green color by August 1—that is, plot 7 had been irrigated just before the actual abandonment of tissue in the spike took place through drying or maturity. By August 3 the color was disappearing on the side florets of plants in plot 2, which had begun to suffer from drouth a few days before. By August 4 the color was apparent only around the furrow of the kernels from this plant, and the lateral florets of plot 3 were

losing color. The plants on plot 3 had exhausted their water supply to the point of wilting badly. Those on plot 4 were affected slightly. This is apparent in the various graphs, but is more significant when correlated with the field observation.

The ripening was not uniform. On most of the plots the bases of the spikes were inclosed in the leaf sheaths. The kernels so inclosed did not ripen as soon as those which were exposed. The kernels from plot 8 were wrinkling by August 5 and therefore were ripe. The tip kernels from all plots were wrinkling by August 8, but the basal kernels in some cases were still adding material. Of the plots irrigated once after June 23, plot 5 was the last to ripen, having sufficient water and having been irrigated before maturity was as far advanced as in plot 7. The later maturity of plot 5 is apparent in figure 18.

The departure in the growth of the various plots came at about the critical stage pointed out in the paper on daily development—that is, 14 days after flowering. The course of the wet weights indicated that the ultimate size of the kernel was affected 3 days earlier. The nature of this change has not been investigated; but, as was suggested, it may be correlated with the stopping of the addition of new cells or with the entering upon the secondary phase of starch formation.

At Aberdeen, the deposit of dry matter continues until just before the grain wrinkles. Maturity at Aberdeen seems to occur at the earliest date possible without accident or drying. In other words, there is no prolonged period of maturation such as apparently takes place in districts where cold, wet weather occurs at ripening time.

CONCLUSIONS

At Aberdeen, Idaho, deposit of dry matter in the kernel continues until very near the point of absolute ripeness.

The plants are able to utilize water up to the date of full maturity. Late irrigation results in a greater activity and a later maturity.

A deficiency of water, even after the spikes are losing their color, results in checking the deposit of dry matter.

A deficiency of water earlier in the development of the kernel probably determines the size of the kernel, even before the rate of deposit of dry matter is checked.

LEAFROLL, NET-NECROSIS, AND SPINDLING-SPROUT OF THE IRISH POTATO[1]

By E. S. SCHULTZ, *Pathologist, Cotton, Truck, and Forage Crop Disease Investigations, Bureau of Plant Industry, United States Department of Agriculture,* and DONALD FOLSOM, *Associate Plant Pathologist, Maine Agricultural Experiment Station*

INTRODUCTION

Potato (*Solanum tuberosum L.*) leafroll of the type that is transmissible but that has not been proved to be parasitic has been differentiated from other types by Appel (*3*)[2], Orton (*15*), Wortley (*24*), and others, and designated as phloem-necrosis by Quanjer (*16*, *17*). It is considered by Quanjer (*17*, *p. 41*) to be an infectious disease caused by a virus or ultramicroscopic parasites. The absence of data concerning its cause and concerning natural and artificial means of its transmission has made it difficult to distinguish sharply between it and various other leafroll diseases of the potato and has resulted often in confusion and conflict in the literature (*3; 15, p. 3, 19, 25, 34; 17; 24*). The reviewing of this literature has been done previously (*15*, *17*, *18*) and is beyond the scope of this paper, which is concerned chiefly with symptoms and transmission.

SYMPTOMS

LEAFROLL

The principal macroscopic characteristics of the type of leafroll[3] considered in this paper include rolling, rigidity, brittleness, leathery texture, light green, yellowish, reddish, or purplish discoloration of the affected leaves; dwarfing of the vines, which usually remain erect and rigid; shortness of stolons; reduction in the number and size of tubers; and rigidity or woodiness of the tubers. Some of these characteristics may be absent at times. The rolling may appear upon the upper leaves alone or only upon the lower leaves or throughout the entire vine. It consists of an upward curving of the sides of each leaflet with the midrib at the bottom of the trough thus formed. (See Pl. 1, A; 2, A.) Its extent depends largely upon the time when infection occurred and upon the age of the affected plant. Plants infected relatively late in their development may show rolling in the upper leaves only, while those

[1] This paper is based upon investigations carried on as a cooperative project between the Office of Cotton, Truck, and Forage Crop Disease Investigations of the Bureau of Plant Industry, United States Department of Agriculture, and the Department of Plant Pathology of the Maine Agricultural Experiment Station. Unless otherwise indicated the work was performed in northeastern Maine in the vicinity of Presque Isle. The order of arrangement of the authors' names is not intended to indicate that one cooperating institution contributed more than the other to the results.

[2] Reference is made by number (italic) to "Literature cited," p. 78-80.

[3] Throughout this paper the term "leafroll" is employed as an abbreviation of "apparently nonparasitic, transmissible leafroll" and as a synonym of "phloem-necrosis."

Journal of Agricultural Research, Washington, D. C. Vol. XXI, No. 1 Apr. 1, 1921 Key No. G-122

becoming infected from the tuber or when only a few centimeters tall show it in the lower leaves first, usually followed by rolling of progressively higher leaves later in the same season until most or all are rolled.

Some other diseases have characteristics in common with leafroll, but they can be distinguished from it. Leafroll is marked by rigidity or stiffness of the affected foliage (Pl. 1, A, B) in great contrast with the flaccid, wilted condition of the rolled leaves found on vines affected with wilt diseases. It causes the leaves to be rolled symmetrically instead of asymmetrically as on plants whose leaves, usually a few top ones, are injured by certain insects. It closely resembles when in the top alone the type of rolling found on plants affected with Rhizoctonia, but the effect of Rhizoctonia will be disclosed by examining more closely especially for the characteristic underground stem lesions. The type of leafroll caused by blackleg usually appears on the entire plant, accompanied by more pronounced yellowish discoloration, and disclosure of the blackened underground stem will distinguish this type further. A nonparasitic type of leafrolling resulting from excessive soil moisture resembles very closely the kind considered in this paper. However, in the former the leaves on the entire plant may become rolled at any time in the development of the vine, the foliage does not become as stiff and rigid, and the leafrolling is limited to segregated areas where soil moisture is excessive. Another nonparasitic type is caused by drouth conditions, but usually is limited to the lowest leaves on the side of the plant most exposed to sunlight and is accompanied by limpness rather than by rigidity of the leaves.

NET-NECROSIS

Orton first used the name "net-necrosis" in connection with an illustration (*15, Pl. II, fig. 2*). As described previously by other writers (*6, 7, 9*), the most apparent effect of this disease in the tuber is a discoloration of the fibrovascular bundles, originating at the rhizome scar. This is dark, varying from brown to black, and is in the form of a network (Pl. 2, B) which may extend throughout the whole tuber. The appearance of affected tubers in section is shown in Plate 3. The writers have seen net-necrosis occasionally absent in the stem end while pronounced in the bud-end half. While it is not difficult in severe cases to distinguish, with the unaided eye, the type of net-necrosis under consideration from wilt types of vascular discoloration (*15, Pl. II*), the writers often have found it very difficult and even impossible to do so in slight and, sometimes, in moderate cases. Recourse to microscopic examination then has been necessary, the phloem being the tissue showing necrosis instead of the xylem. As will be described more in detail later, other leafroll characteristics besides necrosis of the phloem appear to be inseparable from net-necrosis. Net-necrosis tubers are often hard and firm (Pl. 4, A), as are leafroll tubers, and bluish on the stem end. Frost-

necrosis of the net type may have a similar appearance, but the writers have not found any frost-necrosis of the ring or blotch types in their net-necrosis material and have found, as reported by Jones and others (*12, p. 36, 45*), that frost-necrosis induced experimentally (Pl. 4, B) was not accompanied by any of the symptoms characteristic of leafroll.

SPINDLING-SPROUT

As with other descriptive names for diseases for which no pathogene has been described, it is quite probable that with "spindling-sprout" more than one cause is involved. The type considered in this paper is shown in Plates 3, B; 4, A, C; and 5, A.

GEOGRAPHICAL DISTRIBUTION

It may be inferred from the reports on the distribution of leafroll that it occurs wherever the Irish potato is grown. Orton (*15*) mentions its occurrence in Austria-Hungary, Denmark, Germany, Holland, Sweden, Switzerland, and the United States. It is also reported to be in France and Java (*17*). Collaborators for the Plant Disease Survey (*11, p. 53*) have noted its occurrence in the States of California, Colorado, Connecticut, Georgia, Idaho, Iowa, Maine, Maryland, Massachusetts, Michigan, Minnesota, Montana, Nebraska, New Jersey, New York, Ohio, Oregon, Pennsylvania, South Carolina, Tennessee, Utah, Vermont, Washington, and Wisconsin. Wortley (*24*) states that he examined more than 60 varieties of potatoes affected by this disease in America—in the East from Florida to Maine; in the Middle West and West in Michigan, Minnesota, and Colorado; in Canada in the Provinces of Ontario, Quebec, New Brunswick, Nova Scotia, and Prince Edward Island; and in Bermuda.

Data are very few concerning the extent to which net-necrosis is found geographically. Reference to Table VI, and to the authorities already quoted in regard to the symptoms shows that it is found generally in Maine and at least to some extent in other States. A form of spindling-sprout may sometimes be a result of net-necrosis, as will be shown later, and so may possibly be found wherever the latter disease appears.

ECONOMIC IMPORTANCE

Estimates made by the collaborators of the Plant Disease Survey (*11, p. 53*) show that in the United States the percentage of plants affected with leafroll may range from 1 to 95. The presence of the disease in almost all the potato-growing sections, including the most important seed-growing centers, produces a very favorable condition for its continued spread. This is more particularly the case where the agents of its dissemination are most abundant, as indicated in the following pages. Leafroll causes considerable losses wherever an appreciable percentage of the plants are affected, because diseased hills produce tubers which may be greatly reduced in size and number. Plants severely diseased will

produce only culls, and these will result in practically a total loss to the grower. The results of studies dealing with the effect upon yield are given in Table I.

TABLE I.—*Effect of leafroll upon yield*

Lot No.	Variety.	Total number of hills.	Percentage of hills leafroll.	Total yield (in pounds).	Yield rate (in pounds per hill).
1919–AF 17, 18, 19[a]	Irish Cobbler	14	0	20	1.43
1919–AF 30 and 31[a]	do	6	100	5	.83
1920–20	Irish Cobbler, strain A	1,195	0	2,052	1.72
1920–24	do	909	10	1,220	1.34
1920–22	Irish Cobbler, strain B	639	0	943	1.47
1920–23	do	616	3.3	722	1.17
1920–28	do	150	100	37	.25
1920–26 and 29	Irish Cobbler	376	100	153	.41
1920–P. I. 13	do	8	100	4.5	.56
1920–P. I. 15	do	12	0	21	1.75

[a] The year of planting is given as part of the lot number.

In Table I the two 1919 lots and lots 1920–P. I. 13 and 15 were hill-selected and planted according to the hill- and tuber-unit method. The others were planted in bulk. As indicated, in two cases a single strain was divided into two or three lots, which may be compared with greater value than lots from different strains. The difference in yield between the two comparable 100 per cent leafroll lots—those planted in bulk in 1920—is due largely to differences between the strains. It is doubtful whether the small amounts of leafroll in lots 1920–24 and 1920–23 are entirely responsible for the reduction in yield rate as compared with the corresponding healthy lots, 1920–20 and 1920–22. However, it is clear that the yield rate of entirely leafroll stock is very materially reduced as compared with that of healthy lots.

When net-necrosis appears as a symptom of leafroll, tubers which otherwise could be used for culinary or exhibition purposes become of less value. Even the usual severe effects of leafroll upon the plant are accentuated by the phloem-necrosis of the tuber, as shown in Plates 5, B, and 6, A. The comparative infrequency of its appearance makes it less important than leafroll, but its relation to leafroll makes the latter, as the fundamental trouble, still more undesirable.

Plate 7, A, B, shows a row, and Plate 7, C, shows a plot of dwarfed plants produced by net-necrosis seed. The effect of net-necrosis upon the yield is considered in Table II. Data concerning the lots grown at Highmoor Farm (of the Maine Agricultural Experiment Station, in southern Maine) and in 1917 at Aroostook Farm (Station Farm in northeastern Maine) were secured, respectively, by Dr. W. J. Morse, plant pathologist, and Mr. G. B. Ramsey, then assistant plant pathologist. These data, in so far as they are concerned with symptoms, are indicated in the table by quotation marks.

TABLE II.—*Effect of net-necrosis upon yield*

Lot No.[a]	Variety.	Sub-lot No.	Place grown.	Condition of seed and plants.	Amount tested for yield.	Yield rate.	Ratio of yield rate.
1916-D	Green Mountain		Highmoor Farm	"Healthy"		325 bushels per acre	100
1916-R	Rural New Yorker		do	do		do	100
1916-G	Green Mountain		do	"Net-necrosis, leafroll" (Pl. 7, A)	93 hills	100 bushels per acre	31
1916-B	do		do	"Net-necrosis leafroll" (Pl. 7, B)	do	38 bushels per acre	12
1917-D	Green Mountain (Davis strain)		do	"Healthy"	300 hills	244 bushels per acre	100
1917-S	Green Mountain	1	do	"Net-necrosis"	247 hills	110 bushels per acre	45
1917-S	do	2	do	"Not net-necrosis"	16 hills	154 bushels per acre	63
1917-A	do	1	do	"Net-necrosis"	231 hills	134 bushels per acre	55
1917-A	do	2	do	"Not net-necrosis"	180 hills	172 bushels per acre	70
1917-D	Green Mountain (Davis strain)		Aroostook Farm	"Healthy"		274 bushels per acre	100
1917-S	Green Mountain	3	do	"Net-necrosis in some. Many leafroll" (Pl. 7, C)	259 hills	84 bushels per acre	31
1917-A	do	3	do	do	169 hills	101 bushels per acre	37
1918-L	Green Mountain (Lowell strain)		Highmoor Farm	"Healthy"	1/80 acre	221 bushels per acre	100
1918-R	Green Mountain	1	do	"Severely net-necrosis"	do	36 bushels per acre	16
1918-R	do	2	do	"Slightly net-necrosis"	do	145 bushels per acre	66
1919-HM	do		Aroostook Farm	Healthy	¼ acre	2 pounds per hill	100
1919-MM	do		do	Mosaic	do	1.6 pounds per hill	80
1919-HB	Bliss Triumph		do	Healthy	do	1.4 pounds per hill	70
1919-MB	do		do	Mosaic	do	.9 pound per hill	45
1919-48	Green Mountain (Davis strain)		do	Leafroll	11 hills	.75 pound per hill	38
1919-21	Green Mountain		do	do	17 hills	.73 pounds per hill	37
1919-58	do		do	do	48 hills	.69 pounds per hill	35
1919-66	do		do	do	23 hills	.52 pounds per hill	26
1919-39	do		do	Net-necrosis, leafroll	17 hills	.50 pounds per hill	25
1919-47	do		do	do	8 hills	.64 pounds per hill	32
1919-84	Beauty of Hebron [b]		do	do	40 hills	.36 pounds per hill	18
1919-85	Seedling [b]		do	do	12 hills	.46 pounds per hill	23
1919-116	Up-to-Date [b]		Presque Isle Laboratory plots.	do	do	.38 pounds per hill	19
1919-117	Early Six Weeks		do	do	4 hills	.40 pounds per hill	20
1919-118	Sensation [b]		do	do	do	.63 pounds per hill	32
1919-119	Dearborn's [b]		do	do	do	.60 pounds per hill	30
1919-120	Early Sunrise [b]		do	do	8 hills	.07 pounds per hill	4
1919-121	Early Michigan [b]		do	do	do	.20 pounds per hill	10
1919-123	New White Hebron [b]		do	do	24 hills	.56 pounds per hill	28
1919-124	Green Mountain (Davis strain)		do	do	40 hills	.43 pounds per hill	22
1919-125	Green Mountain (Lowell strain)		do	do	96 hills	.54 pounds per hill	27

[a] The year of planting is given as part of the lot number.

[b] Identification made and seed furnished originally by Prof. William Stuart and Mr. P. M. Lombard, of the Office of Horticultural and Pomological Investigations, Bureau of Plant Industry, United States Department of Agriculture. Source of seed in 1919 was Highmoor Farm.

The comparisons in Table II deal with small lots for the most part, chiefly because of the scarcity of net-necrosis material. They indicate that while leafroll without net-necrosis reduces the yield greatly, both together reduce it still more.

TRANSMISSION OF LEAFROLL

TRANSMISSION BY TUBERS

Transmission of leafroll through the tubers has been noted by different investigators studying this malady (*15*, *17*, *22*). Observations made by the writers upon the same strains of leafroll diseased stock since 1916 show that these stocks consistently have developed plants with the characteristic leafroll symptoms. Tuber production has practically ceased in some of these. Others continue to form plants and tubers as in 1916 but always show leafroll.

TRANSMISSION BY GRAFTING

TUBERS

Since mosaic of Irish potatoes was successfully transmitted by the writers by means of tuber grafts (*20*), similar methods were followed with leafroll. In May, 1919, 20 tubers of approximately the same size and shape were selected from healthy and from leafroll stock. The freshly cut surfaces of a healthy half tuber and a leafroll half tuber were brought into intimate contact and were kept there with rubber bands. Planting followed immediately. The other half of each of the healthy tubers was planted separately as a control. A set of 7 tubers grafted with the halves from healthy tubers served as an additional control.

At the end of the growing season all the control plants were free from leafroll. Three of the 20 healthy half tubers grafted on leafroll half tubers had produced plants with leafroll. Upon examination it was found that these 3 were the only ones which had formed organic union with the corresponding diseased halves. One of the 3 plants thus inoculated through tuber grafting, together with the control, is shown in Plate 8. These results confirm similar ones secured by Quanjer (*17*).

STALKS

In the summer of 1919 a healthy stalk in each of three hills of the Green Mountain variety was grafted with a scion taken from a leafroll plant of the same variety. The stalks at the time of grafting were about 16 cm. tall. At the same time and in a similar manner a stalk in each of four Irish Cobbler hills was grafted. These grafts were in the open field, in three 4-hill tuber units.

By the end of the growing season in the seven different grafted hills each of the shoots growing from the stock just below the graft developed

leafroll. At this time the five ungrafted hills from the same tuber units were still free from leafroll. In the fall of 1919 the tubers from these grafted and ungrafted hills were reserved for planting in 1920. Observations on the second-generation plants in 1920 showed that all the tubers from the leafroll grafted vines produced leafroll plants, while those from four of the five ungrafted hills gave rise to healthy vines. The infection of one control hill was probably due to inoculation by aphids in 1919. These results confirm similar ones secured by Quanjer (*17*) with grafts.

In view of results already obtained with aphids and to be described later, grafts that were made in the field in 1920 were covered with insect cages. Three Irish Cobbler tubers were taken from a lot which was rogued in 1919 and which contained less than 1 per cent of leafroll in 1920. Each was cut into 3 pieces, and each tuber unit was planted under a cloth-covered insect cage. Scions from leafroll plants in the open field were grafted on July 15 upon 4 stalks in each cage, 2 in the second and 2 in the third hill of each tuber unit. All the 12 scions but 1 lived until August 25, when the hills were dug. In spite of precautions, one or more individuals of the potato aphid (*Macrosiphum solanifolii* Ashm.)[1] were introduced into each of the first and second cages, with the result that by August 20 such aphids were numerous. None were found in the third cage at any time. The results were the same for all 3 tuber units, and it seems probable that the aphids had not been abundant long enough to contribute to them. On August 25 each of the 6 hills with grafts, except 1 in the second cage, showed leafroll in the top of a branch coming from a stock just below the graft. One such branch and a control are shown in Plate 6, B, C.

TRANSMISSION BY APHIDS

INDICATIONS OF NATURAL TRANSMISSION FROM FIELD OBSERVATIONS

During 1917 each healthy control lot was planted in the same row with, or in an adjoining row to, leafroll stock of the same strain and variety. Leafroll appeared in 1918 in the progeny of hills that during the previous season apparently were free from leafroll. The healthy hill-selected lots were planted in 1918 and 1919 in a section of the plot more apart than in 1917 from the leafroll lots of the same variety, being from 2 to 12 meters distant. Twenty-five per cent of the 438 hills of control lots, representing Green Mountain, Irish Cobbler, Early Rose, and Burbank varieties, showed leafroll in 1918. Only 13 per cent of the 240 control hills, representing the same varieties, were leafroll in 1919. In 1920 the percentage of leafroll hills, from a total of 336 control hills of the same varieties as in 1919, was 12. It is assumed that, as

[1] Identified by Dr. Edith M. Patch, Entomologist of the Maine Agricultural Experiment Station.

with mosaic (*19*, *20*), new infection appearing early in the season is the result of inoculation late the preceding season. It then follows that the decrease in leafroll in 1919 and 1920 in these control lots apparently resulted from the increase in distance from leafroll lots in 1918 and 1919. Leafroll inoculation, although less in 1918 and 1919 than in 1917, could still be made by aphids dispersing from the diseased lots and from the few diseased hills in the control lots.

In addition to the observations made on the foregoing control lots, which were carefully selected hill and tuber units, some were made on stocks planted in bulk. Here the rows were so arranged that two of them, each containing 300 healthy Irish Cobbler hills, were planted on each side of a row of wholly leafroll stock of the same variety. The entire plot then included 5 rows, with leafroll stock in the middle or third row. This test was begun in the season of 1918, when the aphids were very numerous in northeastern Maine. At the end of the season representative separate lots were selected from the apparently healthy rows before the leafroll stock in the third row was dug. In 1919 these lots were planted in separate rows. Observations now disclosed the presence of leafroll in 1 per cent of the stock which in 1918 was grown in the two outer rows. In the stock grown in the two rows next to the leafroll row, 5 and 11 per cent, respectively, developed leafroll in 1919.

The lot which in 1919 was 11 per cent leafroll was again located next a leafroll row in 1919, and the lot 5 per cent leafroll was in the third row from a diseased row. The leafroll plants were rogued from these before the aphids appeared so that the effect of these insects as carriers as well as the effect of removing diseased plants could be ascertained. Examination in 1920 disclosed leafroll in 5 per cent of the stock grown next to leafroll stock in 1919, and leafroll in ½ per cent of the stock grown three rows from leafroll in 1919. In view of the results obtained with aphids as agents of leafroll transmission, described later, the spread of leafroll to healthy stock grown in the vicinity of leafroll plants can reasonably be attributed to these insects. Whatever may be the cause, increase of proximity clearly increased the spread of leafroll in the field, as has been found by Quanjer (*17*), and by Murphy and Wortley (*13*, *14*), and the variation of the spread from place to place and from season to season, as noted by Murphy and Wortley (*14*), is such as might be expected if aphids were the responsible agents.

FIELD EXPERIMENTS WITH INSECT CAGES

Inasmuch as Quanjer (*17*) and the writers regarded leafroll as being a disease of a type similar to mosaic, and as the writers (*19*, *20*) had secured natural transmission of mosaic by means of aphids, it seemed advisable to attempt transmission with leafroll also. Consequently experiments were begun in the summer of 1919 with special precautions taken against the possibility of soil infection. Seventy Green Mountain tubers were

planted in a small plot with the nearest groups of leafroll plants cultivated with different tools and situated at lower elevations at distances of 10, 15, and 40 meters, respectively. The records indicated that no leafroll plants had been grown in the soil of this plot since 1916 or possibly before, and stocks grown in it during 1917 showed no leafroll in 1918 or 1919. Infection from the soil of the plot thus seems to be impossible. No leafroll was present in the plot during 1919, or in the progeny of another bushel lot of the same strain planted elsewhere,[1] except in the progeny of 2 of the 70 tubers. These were grown in two insect cages as 3-hill tuber units. On July 26, spinach aphids (*Myzus persicae* Sulz.)[2] were transferred to these 2 tuber units, respectively, from two caged potato plants grown in pots, the first having leafroll and the second both leafroll and mosaic. The aphids were of a stock originally kept upon radish plants for a number of generations and proved to be nonvirulent in regard to potato diseases (*19, p. 262–264*). After their introduction to the 2 tuber units, the latter before being dug on September 17 showed the external characteristics of leafroll in the top leaves. In 1920 the tubers from these plants were planted with others from the same plot, each being split and producing a 2-hill tuber unit. The observations made in 1920 are summarized in Table III.

TABLE III.—*Results of inoculation with aphids from leafroll plants in field cages in 1919*

Tuber units in 1919.		Tuber units in 1920.	
Total.	Treatment.	Total.	Percentage of leafroll.
42	Caged. No aphids from leafroll plant	500	0
7	Uncaged. Aphids uncontrolled	84	0
1	Caged. Aphids from leafroll plant	[a] 8	63
1	Caged. Aphids from plant with leafroll and mosaic	[b] 7	86

[a] One tuber, both severely net-necrosis and leafroll. For appearance of a leafroll plant of this lot, see Plate 9, A.
[b] 57 per cent mosaic.

Nineteen of the 70 tuber units in this plot are not considered in Table III, being discarded in 1919 at digging time or their progeny being planted in other fields in 1920 and showing no leafroll. It is clear that the introduction of aphids from leafroll plants caused infection and was the only means of transmission of this disease in this plot.[3] Plate 9 shows plants of the second generation of this stock.

[1] Observed by Dr. W. J. Morse.
[2] Identified by Dr. Edith M. Patch.
[3] After the manuscript for this paper had been submitted for publication, a similar and contemporary but entirely independent experiment was reported as giving similar results (BOTJES, Jan Gerhardus Oortwijn. DE BLADROLZIEKTE VAN DE AARDAPPELPLANT . . . viii, 136 p., 8 pl. Wageningen. 1920. Inaug. Diss. Literatuur, p. 118–122. Summary in German, p. 123–136).

GREENHOUSE EXPERIMENTS WITH INSECT CAGES

During the winter of 1919–20, tubers from healthy Irish Cobbler potato plants were split in two and the halves planted in separate pots in the greenhouse at Washington, D. C. When the plants from these half tubers had reached a height of a few centimeters, some of them were inoculated by means of spinach aphids (*Myzus persicae* Sulz.),[1] which were transferred to the leaves after having been brushed from leafroll plants of the same variety into a wide-mouthed bottle. The aphids were allowed to feed for a few weeks before being killed with tobacco fumes. In each case the control plant from the corresponding half of the same tuber was grown under similar conditions and remained healthy. Additional data regarding these inoculations are given in Table IV.

TABLE IV.—*Leafroll inoculations by means of aphids*

Inoculated plants.								Control plants.
Plant No.	Inoculation.			Insect cage.	Date of fumigation.	Date of first symptom.	Later observations.	
	Date.	Number of aphids.	Height of stalks.					
	1920.		*Cm.*					
339a	Feb. 9	About 50	3 to 6	Present to Mar. 5.	Mar. 5	Mar. 5	Apr. 2, severe leafroll.	339b, not caged or fed upon by aphids.
340a	Feb. 19	About 100.	5 to 8	Present...	Mar. 10	Mar. 19	....do.....	340b, like 339b.
350a	Feb. 24	...do.....	4	None.....	Mar. 17	...do.....	.....do.....	350b, like 339b.
351a	...do.....	...do.....	4	...do.....	...do.....	...do.....	.....do.....	351b, like 339b.
353b	...do.....	...do.....	4	...do.....	...do.....	...do.....	.....do.....	353a, about 100 aphids from mustard Mar. 13, when 4 cm. high.
352b	Mar. 2	...do.....	4	...do.....	...do.....	Mar. 31	Apr. 13, severe leafroll.	352a, like 339b.
355a	...do.....	...do.....	4	...do.....	...do.....	...do.....	.....do.....	355b, like 339b.
359a	...do.....	...do.....	4	...do.....	...do.....	...do.....	.....do.....	359b, like 339b.
.....	.....	.....	.....	.....	.....	.....	.....	356a, like 353a.

From the data presented in Table IV it is apparent that the first symptom was noted from 24 to 29 days after inoculation. This consisted of a slight rolling of the lower leaves. Later this and other characteristic leafroll symptoms became severe, consisting of pronounced rolling and stiffness of the lower leaves, rolling in many cases of the majority of the upper leaves, slight marginal reddish discoloration of many leaves, and rigidity of the whole plant. On half the plants the aphids were killed from 9 to 14 days before the first symptoms appeared and in any case from 23 to 27 days before the symptoms were noted as being severe. Moreover, the control plants which were treated with nonvirulent aphids were still free from leafroll when last observed on April 15, so that aphids alone could not be considered as the cause of the leafroll symptoms.

[1] Identified by Dr. A. C. Baker, Entomologist, Deciduous-Fruit Insect Investigations, Bureau of Entomology, United States Department of Agriculture.

One such control is shown in Plate 10 with the corresponding inoculated plant.

On April 15, 1920, the vines were still green but had made practically full growth. At this time the tubers were harvested from each of the inoculated plants as well as from each of the controls in order to note the amount of infection in the plants of the second generation. In June, about two months later, these tubers were planted in the field. Because of the very brief resting period only a few produced vines of sufficient size to be of value for observation. Two of the second-generation plants, one treated in the first generation with aphids from a leafroll plant and the other its corresponding untreated control, are shown in Plate 11. The former shows very marked leafroll, but the latter remained healthy. Of the controls three out of eight were sufficiently large to show that they were free from leafroll. The remainder had made less than 3 cm. growth when a killing frost ended the season; and hence, although apparently healthy, they were too small for notes to be significant. Of the eight plants whose parents were inoculated, five developed marked leafroll symptoms. The remainder, like the controls, were not yet large enough for notes at the end of the season. Even though not every plant in the second generation made growth adequate for observations, yet the fact that the remainder of the vines disclosed such marked differences, healthy in the case of control stock and distinctly leafroll in the case of inoculated stock, confirms the evidence that the leafroll of the first generation was transmitted by aphids.

GREENHOUSE EXPERIMENTS WITHOUT INSECT CAGES

During the winter of 1919–20 when cage experiments with spinach aphids were being conducted in the Washington greenhouse, another set of healthy potato vines was exposed there to aphids dispersing naturally from leafroll plants. The aphids were of two kinds, mixed, most of them being the potato aphis (*Macrosiphum solanifolii* Ashmead)[1] and the rest the spinach aphis.[1] The healthy potato plants thus exposed to aphid inoculation were located in greenhouse A, as is indicated in Table V. They were grown in 8-inch pots which were within 1.5 meters of the aphid-infested leafroll potato vines of the Irish Cobbler and Green Mountain varieties. Aphid dispersal took place freely during the last week in February, 1920, the healthy plants being half grown. In greenhouse B, as is shown in Table V, a control set of healthy plants similar to those in greenhouse A was set among leafroll plants. The conditions in greenhouse B were like those in greenhouse A with the exception that aphids were eliminated by weekly tobacco fumigation.

On April 13, 1920, when the tubers were harvested, two Irish Cobbler plants of series No. 1 and two Green Mountain plants of series No. 2

[1] Identified by Dr. A. C. Baker, of the Bureau of Entomology, United States Department of Agriculture.

showed leafroll. The tubers of these four plants as well as those of the remainder in both greenhouses, were reserved for study of the second-generation plants. The appearance of this second-generation stock in the experimental field plots is indicated in Table V.

TABLE V.—*Transmission of leafroll by aphids dispersing naturally in the greenhouse*

Series No.	Variety.	First-generation plants.			Second-generation plants.		
		Time of planting.	Location of experiment.	Distance from leafroll plants.	Total number.	Number leafroll.	Percentage leafroll.
1	Irish Cobbler	Nov. 28, 1919	Greenhouse A; leafroll plants and aphids present.	0.5 to 1 meter	16	9	56
2	Green Mountain.	Dec. 3, 1919	do	0.5 to 1 meter	7	3	42
3	do	Jan. 12, 1920	do	Next to leafroll plants	8	5	63
4	do	do	do	1.5 meters	18	4	22
5	Irish Cobbler	Jan. 29, 1920	Greenhouse B; leafroll plants but no aphids present.	0.5 to 1.5 meters	13	0	0
6	Green Mountain.	Dec. 18, 1919	do	1.5 to 3 meters	14	0	0

From Table V it is evident that leafroll developed in a high percentage of the progeny of the healthy potato plants subjected to infestation by aphids from leafroll potato vines. On the other hand, it is equally apparent that all the healthy plants not exposed to aphid infestation remained entirely free from leafroll in both the first and second generations. Furthermore, it is clear that a higher percentage of leafroll developed as the plants of the first generation were closer to leafroll plants. It will also be noted that contact of healthy vines with leafroll foliage was neither sufficient nor essential for transmission of this disease, and that there was no contact of roots. The dispersal of aphids from leafroll foliage to healthy foliage was alone effective in transmitting leafroll.

In the spring of 1920, 120 mostly healthy tubers were split into halves and were put into a warm place and caused to sprout. One-hundred of these were used for other experiments, and four of the 100 produced leafroll plants from both halves, as a result of infection of the stock in 1919 or before. The remaining 20 furnished 40 halves. A half from each of the 20 was kept in an individual insect cage for a week together with a leaflet infested, when introduced, with spinach aphids and secured from a diseased potato plant grown in the Maine Agricultural Experiment Station greenhouse at Orono, Me. The aphids varied in number from about 30 to about 100, and at least some of them dispersed to the sprouts, which were from 2 to 5 mm. in length, before being killed by tobacco fumigation. The other half of each tuber was untreated except for similar fumigation. The half tubers were planted without further cutting. Ten halves were fed upon by aphids from mosaic potato foliage; of these,

3 produced mosaic plants as did the corresponding untreated halves, 2 produced healthy plants as did the corresponding untreated halves, 5 produced mosaic plants with the corresponding plants healthy, and none whether treated or not produced a leafroll plant. Ten other halves were fed upon by aphids from leafroll potato foliage; of these, 5 produced leafroll plants while the corresponding halves and the other five pairs of halves produced plants with no leafroll. Thus aphids from leafroll plants inoculated the sprouts of 50 per cent of the half tubers fed upon, while in the control set aphids from mosaic plants inoculated 71 per cent of the half tubers not already diseased. The method used in this experiment is probably not duplicated by natural conditions except for the remote possibility of inoculation at the rhizome scar by aphids reaching and adhering to the tubers at digging time. However, it served to confirm in one generation of plants that which could be proved only by growing the second generation in certain other experiments described in this paper—that is, the ability of aphids to transmit leafroll about as readily as they can transmit mosaic.

TEST OF SOIL TRANSMISSION

In a test regarding the soil harboring of mosaic (*20, Table VIII*), 19 rows of mostly healthy Green Mountain potatoes were planted in 1919 across the location of 14 plots of the preceding year, when 1 plot was of Irish Cobbler potatoes all leafroll and another was of miscellaneous varieties partly leafroll. No leafroll was noted in any of this stock in 1919, or in 1920 except 4 hills in the part of the stock grown on the ground previously planted with miscellaneous varieties. Unless leafroll differs from mosaic by being nontransferable between varieties (*20 p. 324*), these negative results indicate that the danger of leafroll overwintering in the soil is small and is probably due to ungathered diseased tubers which may grow and produce other such tubers and also produce sources for infection by aphids.

Similar negative results in regard to overwintering have been secured by Quanjer (*17*). His explanation of the positive results of proximity on the basis of contamination passing through the soil is, in the opinion of the writers, hardly more plausible than one on the basis of transmission by dispersing aphids. His experiments, as far as can be learned by the writers, were not performed in such a way as to preclude the possibility of inoculation by aphids, and the experience of the writers has shown that with special precautions it is very difficult to control these insects completely and that ordinarily they are abundant. Judging from his figures (*18*), apparent soil transmission was correlated in the first generation with other differences than root contact alone—namely, less complete isolation of the plants by means of pots, more vigorous growth, and a difference in location. All these factors may have influenced the

development and dispersal of virulent aphids.[1] The question of soil transmission will remain open until it is demonstrated with all aerial insects eliminated and even then will be solved more completely when the exact means, possibly either subterranean insects, root contact, soil water, or the soil itself, is disclosed. Wortley (*24*) also reports negative results.

RELATION OF LEAFROLL TO NET-NECROSIS AND SPINDLING-SPROUT

RELIABILITY OF NET-NECROSIS AS AN INDICATOR OF LEAFROLL

A number of separate lots of net-necrosis tubers have been planted in Maine during the past few years, beginning with 1915. The data concerning many of these are given in Table VI. Omission is made of net-necrosis lots which were known to have originated from leafroll hill selection and of those which were grown in the field in 1920. As far as is known, each of the stocks or lots considered in this table is unrelated to the others—that is, no two have had a common origin, though they may have come from the same place. The year of planting is given as part of the lot number. As indicated, sometimes a lot was divided into two or more sublots. The data for all plants grown at Highmoor Farm are taken from records made by Dr. W. J. Morse, and those for the sublots grown in 1917 at Aroostook Farm from records made by Mr. G. B. Ramsey. Such of these as are concerned with symptoms are indicated by quotation marks. The writers are responsible for data for all other lots. In examining this table there should be kept in mind both the difficulty, already discussed in regard to symptoms (p. 48–49), of always ascertaining net-necrosis, or tuber phloem-necrosis, without microscopic examination, and the possibility that plants infected with the leafroll virus may be so reduced in vitality that they lose the usual symptoms of stiffness and pronounced leafrolling. Compare Plate 1, A, B, for the effect of net-necrosis and leafroll in the field, Plate 2, A, and 4, C, for the effect of greater severity of net-necrosis in the greenhouse, and both the two plants of Plate 5, B, and the two pairs of plants of Plate 6, A, for the effect of net-necrosis upon field-grown leafroll hills. The difficulty regarding symptoms would be aggravated by including doubtful cases in a net-necrosis lot, which, when material for study of the disease is rather limited, may seem more desirable than excluding all but marked and severe cases.

The data in Table VI indicate that there is some relation between net-necrosis and leafroll, inasmuch as 26 lots contained both net-necrosis seed and leafroll plants and came from 15 different places and comprised about as many different varieties. The four other lots either contained net-necrosis seed and perhaps leafroll plants (lots 1915–W and

[1] A more recent publication by one of Quanjer's associates (BOTJES, J. G. Oortwijn, op. cit., p. 131) also points out the possibility of insect transmission in the experiments in question.

1915–E) or doubtful cases of net-necrosis and no leafroll plants (lots 1919–54 and 1919–96). It will be noted that whenever all the tubers in a lot were unquestionably or severely affected the plants produced by them were all leafroll or spindling or both.

The preliminary studies having indicated that severe net-necrosis was fundamentally a tuber phloem-necrosis and was always associated with leafroll, attempts were made in 1920 to differentiate more exactly macroscopically between net-necrosis and various types of vascular discoloration not associated with leafroll. A tuber was considered as showing at least a medium stage of net-necrosis if a longitudinal section disclosed vascular discoloration exceeding 1 cm. in extent from the rhizome scar, running through several layers, lacking uniformity in degree of discoloration, and with soggy-looking parenchyma near by. It was considered as being in the severe stage if in addition to the foregoing the discoloration extended into the bud-end half or extended beyond the stem-end third with many of the strands black.

During the planting season of 1920, about 8,000 tubers were examined for the presence of net-necrosis and were planted. Of these, 75 were recorded as being in the severe stage, 89 in the medium, and 87 in either the severe or medium stage with no distinction made. Of the 75, all produced leafroll plants except 3 which did not grow above ground. Of the 89, all but 2 produced leafroll plants. One of the 2 exceptions was among the unusual cases showing the disease only in the eye-end half of the tuber. The second was dug July 26 with another net-necrosis hill of the same lot. It was flabby, with the discolored strands hard and brittle and containing fungous hyphae, discolored xylem, and very little discolored phloem, while the tuber that produced a leafroll plant was rigid, with the discolored strands smaller, more numerous, more extensive, lighter in color, not hard, and containing neither apparent fungous hyphae nor discoloration outside the phloem. It evidently had not been possible to distinguish readily at the time of planting between a wilt tuber and a phloem-necrosis tuber. Of the 87, all but 3 produced leafroll plants, 2 of the exceptions producing wilt plants and the third probably being a wilt tuber.

The practical restriction of net-necrosis diagnosis to leafroll potatoes as just described is made more striking by the following facts. Of the 8,000 tubers examined and planted, 1,000 came from about 10 lots which in 1919 were grown so as to be readily exposed to leafroll infection, or were controls to such lots, and furnished 135 of the diseased tubers, while the remaining 7,000 came mostly from lots concerned with the study of mosaic and furnished only 116 diseased tubers. Furthermore, each of the latter group of 116 tubers came from a lot that either was partly leafroll in 1919 or was artificially inoculated in some way with leafroll, or was near—not exceeding 12 meters at the most—to leafroll lots in 1919.

TABLE VI.—*Lots planted for preliminary study of net-necrosis*

Lot No.[a]	Source.	Variety.	Sub-lot No.	Degree of net-necrosis.	Amount planted.	Place of growing.	Appearance of plants.
1915–W	Ellsworth, Me.	Unknown (white)		"Some not bad"	16 pounds	Highmoor Farm	"Few weak hills."
1915–E	Wells Beach, Me.	Unknown (long red)		"Severe"	8 pounds	do	"All small and weak."
1916–G	Gardiner, Me.	Green Mountain		"Some in all"	204 hills	do	"90 per cent weak and spindling throughout the season." Appear like typical leafroll plants in photograph (Pl. 7, A).
1916–B	Foxcroft, Me.	do		do	119 hills	do	"72 per cent like the 90 per cent of the preceding lot" (Pl. 7, B).
1917–S	South Windham, Me.	do	1	"Present"	314 hills	do	"96 per cent weak and spindling."
Do	do	do	2	"Absent"	27 hills	do	"56 per cent weak and spindling."
Do	do	do	3	"Present in some"	340 hills	Aroostook Farm	"Many plants spindling and dwarfed with a tendency to leafroll" (Pl. 7, C).
1917–A	Kennebunkport, Me.	do	1	"Present"	329 hills	Highmoor Farm	"84 per cent weak and spindling."
Do	do	do	2	"Absent"	243 hills	do	"37 per cent weak and spindling."
Do	do	do	3	"Present in some"	200 hills	Aroostook Farm	"Many plants spindling and dwarfed with a tendency to leafroll" (Pl. 7, C).
1918–R	Brunswick, Me.	do	1	"Severe"	112 hills	Highmoor Farm	"Small and spindling."
Do	do	do	2	"Slight"	125 hills	do	"Healthy."
Do	do	do	3	Present	About 40 hills	Aroostook Farm	Many leafroll.
1918–13, 14	Minnesota	Early Ohio		Present in some	Not stated	do	Most leafroll.
1918–15, 16	do	Irish Cobbler		do	do	do	Do.
1918–18, 19	do	Rural New Yorker		do	do	do	Some leafroll.
1919–G	Greene, Me.	Green Mountain		Severe	1 tuber	Orono greenhouse	Leafroll.
1919–5	Aroostook Farm	Bliss Triumph		Medium in 2 per cent of tubers.	872 hills	Aroostook Farm	Leafroll in 9 per cent of the hills.
1919–54	do	Green Mountain		Slight (?) in 23 per cent of tubers.	61 tubers (whole)	do	None leafroll.
1919–84	Aroostook County, Me.	Beauty of Hebron [b]		Medium to severe	20 tuber units	do	All leafroll.
1919–85	Aroostook Farm	(Seedling) [b]		Severe	3 tuber units	do	Do.
1919–96	Presque Isle, Me.	Green Mountain		Slight (?)	2 tubers (whole)	do	None leafroll.
1919–116	Highmoor Farm	Up-to-Date [b]		Severe or decided	4 tuber units	Presque Isle Laboratory plots.	All leafroll.
1919–117	do	Early Six Weeks		do	1 tuber unit	do	Do.
1919–118	do	Sensation [b]		do	do	do	Do.
1919–119	do	Dearborn's [b]		do	do	do	Do.
1919–120	do	Early Sunrise [b]		do	2 tuber units	do	Do.
1919–121	do	Early Michigan [b]		do	do	do	Do.
1919–123	do	New White Hebron [b]		do	6 tuber units	do	Do.
1919–124	do	Davis Green Mountain		do	10 tuber units	do	Do.
1919–125	Bucksport, Me.	Lowell Green Mountain		do	24 tuber units	do	All leafroll. (See Pl. 2, A.)
1919–CF	Aroostook Farm	Green Mountain		Severe in few tubers.	1,600 hills	Aroostook Farm	3 per cent leafroll.

1920–D	East Union, Me	do		Severe	2 tubers	Orono greenhouse	Leafroll.
1920–A	Bath, Me	Spaulding Rose		Marked	do	do	Do.
1920–G	Wells, Me	Green Mountain		Severe	1 tuber	do	Leafroll; very spindling (Pl. 4, C).
1920–V	Nobleboro, Me	Green Mountain (?)		do	3 tubers	do	Leafroll.

[a] The year of planting is given as part of the lot number.

[b] Identification made and seed furnished originally by Prof. William Stuart and Mr. P. M. Lombard, of the Office of Horticultural and Pomological Investigations, Bureau of Plant Industry, United States Department of Agriculture.

POSSIBILITY OF A COMMON CAUSE OF LEAFROLL AND NET-NECROSIS

In the preceding section of this paper data have been submitted showing that in Maine net-necrosis has been consistently accompanied by leafroll. It may be that net-necrosis, a tuber phloem-necrosis, is caused by the same virus[1] as is leafroll or phloem-necrosis. This hypothesis will be tested further by detailed microscopic studies now under way and by various inoculation experiments begun in 1919, but it explains the available facts and explains them at least as well as does the assumption that the two diseases are caused by different viruses.

Experiments indicate that net-necrosis is apparently nonparasitic in nature and transmissible, like mosaic and leafroll. Numerous attempts by the writers and by others in the same laboratories to find one kind of organism associated consistently with the disease have resulted only in failure. The usual origin of discoloration at the rhizome scar indicates that the source of infection comes from the parent plant. The rare cases already noted as found by the writers in which the phloem discoloration was restricted to the eye-end portion suggest that the disease is carried with the juice. Transmissibility by aphids was demonstrated in the field experiment with insect cages, described on page 54. The leafroll plants from which the insects were taken had been produced by net-necrosis tubers. At planting time in 1920, severe net-necrosis was found in one of the eight tubers from the plant given the third treatment described in Table III, while none was found in the 584 control tubers. The fact that this single tuber showed net-necrosis is explained easily by the theory that one virus causes leafroll and, in the proper conditions, net-necrosis as well.

Correlation between the amount of net-necrosis and leafroll in a number of stocks grown in 1920 has been partly indicated on page 60. This correlation is shown further by data upon the 1,000 tubers in the 10 lots that supplied the majority of the net-necrosis tubers, given in Table VII.

TABLE VII.—*Leafroll and net-necrosis in 1920 in lots healthy in 1919*

Lot No.	Total number of tubers.	Tubers producing leaf-roll plants.		Tubers showing net-necrosis at planting time.	Percentage of leafroll tubers showing net-necrosis.
		Number.	Percentage.		
L-31	227	15	7	2	13
L-34	146	0	0	0	.....
L-37	139	2	1	1	50
L-38	120	15	13	9	60
L-39	102	87	85	62	71
352	111	55	50	36	65
354	50	10	20	5	50
355	55	0	0	0	.....
357	38	22	58	15	68
358	40	6	15	5	83

[1] See p. 74, with footnote, for the writers' use of the term "virus."

A close relation between the two diseases is manifested by facts given in Table VII and elsewhere in this paper. Net-necrosis is never present in lots free from leafroll, is never more abundant than leafroll in lots containing both diseases, and is restricted to the tubers transmitting leafroll. This is in contrast with the usual independence of mosaic and leafroll among lots selected as healthy. Consequently there seems to be a closer relation between net-necrosis and leafroll than between mosaic and leafroll. These facts are hard to explain if net-necrosis is considered to be a disease separate from leafroll, but they are easily reconciled with the theory that the leafroll virus may cause net-necrosis under certain conditions.

This theory may seem to be discredited by the following facts. Leafroll hills usually produce small tubers, but net-necrosis often is found in large ones. Also, net-necrosis often disappears entirely or almost so from a stock while the leafroll remains. Both these questions will be considered in the discussion upon the effect of various factors upon the appearance of net-necrosis, where it is shown that large net-necrosis tubers may come from hills that contracted leafroll late in the season and that in some strains net-necrosis may be largely inheritable. Furthermore, the disappearance of net-necrosis in some varieties might well be expected if it is merely a leafroll symptom brought out by certain conditions.

In this connection it may be pointed out that the indication of leafroll by stem-end browning of tubers was considered by Orton (*15, p. 22*) as no longer being reliable. This conclusion is apparently applicable to stem-end browning in general. It might seem to be warranted even in regard to the net-necrosis type when net-necrosis is absent as a leafroll symptom in certain conditions, to be described in the following sections of this paper, and when net-necrosis modifies the usual appearance of leafroll plants, as described on p. 60.

INFLUENCE OF VARIOUS FACTORS UPON THE APPEARANCE OF NET-NECROSIS

VARIETY, TUBER WEIGHT, AND OPPORTUNITY FOR LEAFROLL INFECTION

It may be noted that in the three lots (L-39, 352, and 357) of Table VII that are more than 50 per cent leafroll the percentage of leafroll tubers showing net-necrosis varies only from 65 to 71. Apparently when the number and percentage of leafroll tubers are high, the conditions governing the development of net-necrosis in such tubers may determine the relative amounts of the two diseases within somewhat narrow limits. In order to determine what factors might influence the development of net-necrosis, comparison was made between different parts of each of a number of lots of which most were divided in 1919 first according to the presence or absence of net-necrosis when planted and later according to the presence, absence, or proximity of leafroll hills in the lot or field. These lots were grown in 1919 either at Aroostock Farm or at the Presque Isle Laboratory plots. During that season all net-necrosis tubers planted at the latter place were in one row at the side of the plot. The tubers were examined for net-necrosis in the spring of 1920, and many of them were planted. The results of the various observations are given in Table VIII.

TABLE VIII.—*Relation of leafroll infection to net-necrosis*[a]

1919.								1920.			
Lot No.	Variety.	Place grown.	Sub-lot No.	Leafroll.	Net-necrosis at planting time.	Nearest leafroll hills.	Nearest net-necrosis hills.	Lot No.	Total number of tubers.	Percentage of tubers leafroll.	Percentage of tubers net-necrosis at planting time.
11	Green Mountain	Aroostook Farm	1	All hills (Pl. 6, A)	All tubers (stem-end sets planted).			L-7	47	.....	28
			2	.....do	All tubers (bud-end sets planted).			L-8	83	.....	20
			3	Absent	Absent	Next or near in row	As for leafroll hills	L-9	74	.....	3
15	.....do	.....do	1	All hills				L-10	22	.....	5
			2	5 per cent removed				L-3	640	0.2	0
			3	5 per cent				L-4	610	4	0.7
110	.....do	.....do	1	Absent	Absent (half tubers planted).	Alternating in row (Beauty of Hebron variety).	As for leafroll hills	L-31	227	7	1
			2	.....do	Control halves to sub-lot 1.	Not alternating	.....do	L-34	146	0	0
126	Green Mountain (Gilbert strain).	Presque Isle Laboratory plots.	1	3 per cent	Absent	Alternating in row (Green Mountain variety, Davis strain.)	.....do	L-39	102	85	61
			2	3 per cent	.....do	1 meter (Irish Cobbler variety).	30 meters	L-38	120	13	7
			3	Absent	.....do	Sublot 1, next section of row.	As for leafroll hills	L-37	139	2	1
V-126	Rural New Yorker No. 2.	.....do	1	All hills	.....do		18 meters	361-A	5	.....	0
			2	4 per cent discarded	.....do	Discarded 4 per cent[b]	.....do	[c]V-126	.....	13	.....
								[d]49-G	5	0	0
V-127	.....do	.....do	1	All hills	.....do		.....do	360-A	5	.....	0
			2	4 per cent discarded	.....do	Discarded 4 per cent[b]	.....do	[c]V-127	.....	1	.....
								[d]49-H	5	20	0
V-134	Early Michigan	.....do	1	All hills	All tubers			L-27	7	.....	0
			2	.....do	Absent		14 meters	365-A	10	.....	0
			3	13 per cent discarded	.....do	Discarded 13 per cent[b]	.....do	[c]V-134	.....	40	.....
								[d]49-H	6	67	67

V-135	Burbank	do	1	All hills	do		do	362	10		10
			2	21 per cent discarded	do	Discarded 21 per cent[b]	do	[c]V-135		21	
								[d]49-M	5	40	0
V-136	Sir Walter Raleigh	do	1	All hills	do		do	363	10		10
			2	6 per cent discarded	do	Discarded 6 per cent[b]	do	[c]V-136		18	
								[d]49-O	5	20	0
V-138	Green Mountain (Davis strain)	do	1	All hills	All tubers			L-30	64		59
			2	do	Absent	12 meters		351	80		45
			3	Absent	do	Next in row	do	352	110	50	32
V-139	Green Mountain (Lowell strain)	do	1	All hills	All tubers			L-28	27		93
			2	do	Absent	12 meters		353	30		93
			3	Absent	do	Next in row	do	354	50	20	10
			4	do	do	Near in row	do	355	55	0	0
V-142	Dearborn's	do	1	All hills	All tubers			L-25	12		0
			2	do	Absent	11 meters		364	35		0
			3	25 per cent discarded	do	Discarded 25 per cent[b]	do	[c]V-142		42	
								[d]49-P	5	60	0
V-143	Up-to-Date	do	1	All hills	All tubers			L-22	17		0
			2	do	Absent	11 meters		365	30		0
			3	30 per cent discarded	do	Discarded 30 per cent[b]	do	[c]V-143		71	
								[d]49-Q	5	80	0
V-144	Sensation	do	1	All hills	All tubers			L-24	8		0
			2	do	Absent	11 meters		366	15		0
			3	6 per cent discarded	do	Discarded 6 per cent[b]	do	[c]V-144		0	
								[d]49-R	5	0	0
V-148	New White Hebron	do	1	All hills	All tubers			L-29	59		0
			2	do	Absent	8 meters		356	22	100	0
			3	Absent	do	Next in row	do	357	38	58	39
			4	do	do	Near in row	do	358	40	15	13
V-154	Peach Blow	do	1	All hills	do	5 meters		367	43		0
			2	24 per cent discarded	do	Discarded 24 per cent[b]	do	[c]V-154		17	
								[d]49-U	5	0	0
V-155	Early Sunrise	do	1	All hills	All tubers			L-26	2		0
			2	Absent	Absent	6 meters	6 meters	[c]V-155		0	
								[d]49-V	5	0	0
V-156	Early Six Weeks	do	1	All hills	All tubers			L-23	7		0
			2	do	Absent	6 meters		368	20		0
			3	18 per cent discarded	do	Discarded 18 per cent[b]	do	[c]V-156		6	
								[d]49-SS	6	17	17

[a] Absence of an entry indicates that the datum was not available or is obvious. Many sublots leafroll in 1919 were not planted in 1920 because of the repeated demonstration of the inheritability of the disease, assumption being made that all their tubers would produce leafroll plants. It is obvious that when a lot was all diseased the distance to the nearest diseased lot would be zero.

[b] Discarded during the second week of August.

[c] Part planted in bulk without careful examination for net-necrosis.

[d] Part planted in tuber units after examination for net-necrosis.

An examination of Table VIII discloses that net-necrosis was inherited only in three Green Mountain lots (11, V–138, and V–139). That is, the sublot which was selected as showing net-necrosis in 1919 developed as much disease in 1920 as was shown by any other sublot, or more. However, in the majority of such sublots (in lots V–134, V–142, V–143, V–144, V–148, V–155, and V–156) there was no net-necrosis in 1920, although in three lots (V–134, V–148, and V–156) varietal susceptibility was shown by the fact that some tubers were net-necrosis that were produced by plants becoming infected with leafroll in 1919. This difference between lots in the inheritability of net-necrosis, apparently varietal, might, however, seem to be due possibly to a difference in the weights of the tubers harvested. This question is considered, for the sublots just previously mentioned, in Table IX. It is seen in Table IX that by far the greater number of tubers in all lots were small. Therefore the tendency to inherit net-necrosis was varietal rather than due to any tuber weight.

TABLE IX.—*Relation between tuber weight and net-necrosis at the time of planting in sublots selected for net-necrosis a year previously*

Lot No.	Sublot No.	Percentage of net-necrosis.	Number of tubers weighing—						
			2 ounces.	3 ounces.	4 ounces.	5 ounces.	6 ounces.	7 ounces.	8 ounces.
11	1	28	26	14	3	3	1	.....	.....
	2	20	44	25	9	3	1	1	.....
V–134	1	0	4	3	.....	.....	.....	.....	.....
V–138	1	59	25	24	13	1	.....	.....	1
V–139	1	93	16	6	5	.....	.....	.....	.....
V–142	1	0	8	4	.....	.....	.....	.....	.....
V–143	1	0	11	5	1	.....	.....	.....	.....
V–144	1	0	1	4	2	1	.....	.....	.....
V–148	1	0	41	9	9	.....	.....	.....	.....
V–155	1	0	1	1	.....	.....	.....	.....	.....
V–156	1	0	7	.....	.....	.....	.....	.....	.....

The effect of recency of infection is revealed in Table VIII in lot V–148. No net-necrosis was shown by the 1920 generation of the sublots selected in 1919 on account of the presence of net-necrosis or of leafroll, while the second generation of the sublot selected in 1919 as healthy hills next in the row to leafroll hills contained many net-necrosis tubers of which about three-fourths were affected severely (Pl. 12, A). Apparently in this stock and variety, net-necrosis was dependent upon leafroll inoculation that occurred not earlier than during the preceding season. The possibility of the differences between sublots 2, 3, and 4 of lot V–148 being due also to a difference in tuber weight is considered in Table X.

TABLE X.—*Relation between tuber weight, recency of leafroll infection, and net-necrosis at the time of planting, in sublots of lot V–148, New White Hebron variety*

Sub-lot No.	Condition of plants in the previous season.	Number of tubers weighing—										Percentage of net-necrosis.
		1 ounce.	2 ounces.	3 ounces.	4 ounces.	5 ounces.	6 ounces.	7 ounces.	8 ounces.	9 ounces.	10 ounces.	
1	Leafroll, from net-necrosis tubers	41	9	9	.....	.....	.....	.....	.....	.....	.....	0
2	Leafroll	2	13	4	1	1	1	.....	.....	.....	.....	0
3	Healthy, next to leafroll hills in same row	.....	10	8	9	6	2	2	.....	1	.....	40
4	Healthy, near leafroll hills in same row	.....	6	11	10	7	3	1	2	.....	1	13

It is evident from Table X that while the tubers are smaller in the sublots free from net-necrosis, there is sufficient overlapping to indicate that recency of leafroll infection was the dominant factor in this lot. Such recent inoculation was followed by net-necrosis also in lots 11, 110, 126, V–134, V–138, V–139, and V–156, but not in lots V–127, V–135, V–136, V–142, and V–143. The tendency for the tubers to be lighter in weight as leafroll is more pronounced is not surprising in view of the previous discussion of the effects of leafroll.

Lot V–148 also shows the importance of proximity to leafroll hills. The progeny of the sublot from healthy hills next to leafroll hills contained three times as much net-necrosis (in terms of percentage of tubers diseased) in correlation with four times as much leafroll as was shown by the progeny of the sublot from healthy hills near leafroll hills. In addition, both lots were 8 meters from the nearest net-necrosis lot.

The previous discussion has disclosed the dominance of varietal and recent-inoculation factors over the tuber-weight factor in regard to net-necrosis. The question then arises how much correlation may exist between tuber weight and net-necrosis, and incidentally leafroll infection, among the tubers of any sublot coming from hills in uniform conditions of growth and showing a high percentage of net-necrosis. Such data are given in Table XI. Here the smallest tubers are dealt with first, and more tubers in the sublot are included as progressively larger sizes are considered. For example, the first entry represents a sublot with 70 tubers weighing 2 ounces, 39 weighing 3 ounces and bringing the total considered up to 109 as given in the column headed by "2 to 3," 12 weighing 4 ounces, and so on. The classes of heavier tubers contain fewer individuals and if dealt with separately would fluctuate too much—from 0 to 100 per cent—to permit ready perception of the effect of a gradual increase of the average tuber weight upon the percentage of net-necrosis and of leafroll.

TABLE XI.—*Relation between tuber weight, net-necrosis, and leafroll infection at the time of planting* [a]

1919.			1920.																													
			Total number of tubers weighing—										Percentage of net-necrosis tubers weighing—										Percentage of leafroll tubers weighing—									
Lot No.	Sublot No.	Conditions.	2 ounces.	2 to 3 ounces.	2 to 4 ounces.	2 to 5 ounces.	2 to 6 ounces.	2 to 7 ounces.	2 to 8 ounces.	2 to 9 ounces.	2 to 10 ounces.	2 to 11 ounces.	2 ounces.	2 to 3 ounces.	2 to 4 ounces.	2 to 5 ounces.	2 to 6 ounces.	2 to 7 ounces.	2 to 8 ounces.	2 to 9 ounces.	2 to 10 ounces.	2 to 11 ounces.	2 ounces.	2 to 3 ounces.	2 to 4 ounces.	2 to 5 ounces.	2 to 6 ounces.	2 to 7 ounces.	2 to 8 ounces.	2 to 9 ounces.	2 to 10 ounces.	2 to 11 ounces.
11	1, 2	Net-necrosis and leafroll...	70	109	121	127	129	130	....	....	....	....	27	24	25	24	23	23	....	....	....	....	....	....	....	....	....	....	....	....	....	..••
126	1	3 per cent leafroll, between net-necrosis leafroll hills.	14	37	58	71	84	91	99	101	102	....	43	46	53	55	58	58	59	60	61	....	79	78	81	83	86	85	85	85	85	....
V–138	1	Net-necrosis and leafroll...	25	49	62	63	63	63	64	....	....	....	68	65	62	60	60	60	59	....	....	....	....	....	....	....	....	....	....	....	....	....
V–139	1	.....do.....	16	22	27	....	....	....	....	....	....	....	94	95	93	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
V–148	3	Healthy next to leafroll hills in same row.	10	18	27	33	35	37	37	37	37	38	20	22	33	39	43	41	41	41	41	39	30	33	44	55	57	57	57	57	57	58
V–148	4	Healthy near leafroll hills in same row.	6	17	27	34	36	37	39	39	40	....	0	12	11	15	14	14	13	13	13	....	0	12	11	18	17	16	15	15	15	....

[a] Leafroll infection in tubers was ascertained from the appearance of their plant progeny in the early part of the season.

In the 1920 generation of the three sublots that showed net-necrosis in 1919—that is, the first, third, and fourth as given in Table XI—the inclusion of progressively larger sets of tubers tends to reduce the percentage of net-necrosis. Thus, inherited net-necrosis is less common as the average tuber weight is greater. In the 1920 generation of the other three sublots a progressive increase in tuber weight is accompanied by a rather marked increase in the percentage of both leafroll and net-necrosis until 5 or 6 ounces are reached, except in sublot 1 of lot 126, where the increase of tuber weight has more effect on net-necrosis percentage than on leafroll percentage. Here, in the sublots with initial net-necrosis, the fundamental relation is one between leafroll infection and tuber weight, with its exact cause unknown. Initial net-necrosis shows a similar relation to tuber weight because it is proportional to leafroll infection.

It has been pointed out that inheritability of net-necrosis tends to be varietal. Inherited net-necrosis may tend to be more common as the tubers are lighter in weight. Recency of leafroll infection may determine the development of net-necrosis within a given variety. Finally, net-necrosis resulting from recent leafroll infection may tend in a given strain to be more common as the proximity to leafroll hills is greater and to be less common in the lighter-weight tubers, both usually in correlation with a similar tendency shown by the leafroll infection itself.

It may also be pointed out that there was a great difference in leafroll infection, as shown in Table VIII, between the first sublot of lot 126 and that of lot 110. This was not necessarily due to the facts that in lot 126 the healthy hills were of the same variety (Green Mountain) as the diseased hills alternating with them and that in lot 110 they were of the Green Mountain variety, while the diseased ones were not. The latter lot, showing much less leafroll (and net-necrosis) in 1920, was in a field in 1919 in which aphids were later in appearance and fewer in numbers than they were in the plot in which the former lot was grown. Also, it was over 150 meters from the weedy border of the field, while the former lot was about 25 meters from one end of an acre plot with a permanent weed patch at both ends and along one side and so was much nearer to the probable sources of newly hatched aphids. The most important difference seems to have been that of abundance of aphids, which have been shown to be capable of transmitting leafroll.

TEMPERATURE

Jones and others (*12*) have demonstrated that a type of net-necrosis may be induced by certain conditions of low temperature, but have distinguished (*12*, *p. 22*) between frost-necrosis of the net type and inheritable net-necrosis. The same distinction is made by Coons (*7*, *p. 37*). One of the writers at Orono followed the methods of Jones and his coworkers (*12*), except that outdoor conditions were used, and induced

TABLE XII.—*Presence of net-necrosis in unchilled tubers*

Lot No.[a]	Sub lot No.	Place grown.	Variety.	Condition of seed and plants.	Date examined.	Number of tubers.	Percentage of net-necrosis.
1916-G		Highmoor Farm	Green Mountain	"Net-necrosis, mostly leafroll"	Jan. 4, 1917	148	11
1916-B		do	do	do	do	127	2
1917-S	1	do	do	"Net-necrosis"	Feb. 15, 1918, or before	120	23
1917-A	1	do	do	do	do	112	19
1917-A	2	do	do	"Grown near lot 1917-A, sublot 1"	Feb. 15, 1918	80	20
1917-D		do	Green Mountain (Davis strain)	"Healthy, next to lots 1917-S, sublot 1, and 1917-A, sublot 1."	do	100	13
1917-AF3		Aroostook Farm	Green Mountain	No notes on leafroll. In same plot with scattered leafroll lots.	Feb., 1918	15	13 (severe).
1918-S and 1918-A	2 1	do	do	Net-necrosis, 65 per cent leafroll	Sept. 15, 1918 (harvest) Dec. 7, 1918 Feb. 7, 1919 Apr. 5, 1919	100	1 49 66 70
1918-S	4	do	do	45 per cent leafroll	Sept. 15, 1918 (harvest) Dec. 7, 1918 Feb. 7, 1919 Apr. 5, 1919	50	0 22 36 40
1918-A	4	do	do	63 per cent leafroll	Sept. 15, 1918 (harvest) Dec. 7, 1918 Feb. 7, 1919 Apr. 5, 1919	50	6 8 16 20
1918-R	1	Highmoor Farm	do	Severe net-necrosis, some leafroll	Feb. 22, 1919	71	7
1918-R	2	do	do	Healthy, next to lot 1918-R, sublot 1	do	127	11
1919-5		Aroostook Farm	Bliss Triumph	Leafroll; harvested Aug. 7	Jan., 1920	50	2
1919-11		do	Green Mountain	Net-necrosis, leafroll; harvested Aug. 7	do	30	7
1919-125		do	Green Mountain (Lowell strain)	Net-necrosis, leafroll; harvested Sept. 11	do	271	13 (4 severe).
1919-84		do	Beauty of Hebron	Net-necrosis, leafroll; harvested Aug. 30	do	110	5

[a] The year of planting is given as part of the lot number.

frost-necrosis of the net (Pl. 4, B), ring, and blotch types. Neither of the last two types of injury has been seen in connection with the leafroll type of net-necrosis, which has developed in connection with leafroll tuber transmission under normal conditions of growing, harvesting, and storing, while at the same time thousands of other tubers, healthy in regard to leafroll, were in the same conditions but remained free from net-necrosis. Moreover, a number of lots of tubers have been selected from stocks grown at Aroostook Farm and Highmoor Farm for the study of net-necrosis or leafroll and have been kept in well-heated buildings, so that it was known that there was no chance for chilling after harvesting. These are described in Table XII. Notes upon the first seven sublots were taken by either Dr. W. J. Morse or Mr. G. B. Ramsey. The sources of many are described in Table VI.

It is seen from Table XII that net-necrosis may develop without any exposure to chilling temperatures. Furthermore, a certain test indicates that there is no relation between higher temperatures of storage and the prevalence of net-necrosis. This test consisted of dividing the tubers from lot 1919–125 of Table XII into eight parts so that the range and average of the tuber weight were as nearly alike as possible for the various sublots. Four sublots were kept in constant temperature chambers at 30°, 25°, 15°, and 8° C., respectively. The other four were kept where the temperature fluctuated daily, the daily means averaging 25°, 21°, 15°, and 10°. This was done for about two months, from November 1 to January 7. At the end of this period examination of the tubers disclosed no differences between the various sublots in regard to net-necrosis that were correlated with differences in temperature.

PHYSIOLOGICAL CHANGES

It may be noted that three lots considered in Table XII were examined at the time of harvesting and at bimonthly intervals afterwards. The percentage of net-necrosis increased markedly up to about the middle of February. Cook (*6, p. 26*) reports that this discoloration may be absent at the time of digging but may develop in storage. Apparently changes that occur during the dormant period of the tubers may be involved with the development of the discoloration.

During preliminary examination of net-necrosis tubers in comparison with healthy tubers, it was found that blackening appeared more quickly in cut or crushed tissues of the former tubers than in those of the latter and appeared more quickly than is possible for bacterial growth. The blackening substance was present in uninjured tissues only in the phloem of those with net-necrosis. It affected protoplasm and protein granules but not starch grains. It did not pass through the walls of vessels in the xylem of healthy tuber segments which were allowed to absorb some of the discolored juice. It developed most rapidly in crushed tissues exposed to the air and was characterized by being associated with acid

coloration in litmus solution when from net-necrosis tubers but not when from healthy tubers. Possibly the discoloration of net-necrosis is due to an accentuation of a normal tendency of the potato tuber tissues to darken upon exposure to air. Darkening has been attributed by Bartholomew (*4*) in the case of blackheart to melanin or humin formed by the interaction of tyrosinase and tyrosin in the presence of oxygen. It may possibly be due, in net-necrosis, to identical or similar physiological changes resulting from, or productive of, leafroll infection. This is indicated by the finding of tyrosinase in greater quantities in leafroll tubers (*8*).

RELATION OF NET-NECROSIS TO SPINDLING-SPROUT

In the preceding sections of this paper evidence has been submitted indicating that net-necrosis of one kind is a symptom of leafroll infection. It may be a cause of spindling-sprout, and the latter may thus become a symptom of leafroll. Spindling-sprout was distinctively pronounced in the net-necrosis half of the tuber shown in Plate 5, A. It was consistently characteristic of the net-necrosis tubers selected from lot V–148, sublot 3, of Table VIII, half of which sublot is shown in Plate 12, A, and was accompanied by a reduction in the number of lengthened sprouts. Such reduction in length is also apparent to some extent in sprouts of the companion sublot 2 from leafroll hills, but they show no decided spindliness (Pl. 12, B). Plate 3, B, depicts the appearance of representative tubers from the two groups shown in Plate 12, A. Plate 4, A, illustrates the accompaniment of net-necrosis and another leafroll symptom—namely, maintained rigidity of the tuber—by spindling-sprout in diseased tubers kept with healthy ones in an uncooled room from June 1 to August 11. The type of spindling-sprout caused presumably by net-necrosis has been described also by Stewart and Sirrine (*23, p. 140–141*) and other types with apparently different causes by the same writers (*23*), by Coons (*7, p. 29*), and by Haskell (*10, Pl. 13, Fig. B*).

RELATION OF LEAFROLL TO MOSAIC

As indicated previously, Quanjer considers that both mosaic and leafroll are virus diseases. The writers are of the same opinion. That is, they consider both to be transmissible or infectious diseases for which no pathogene or other cause has been isolated or synthesized.[1]

Regardless of such similarity between the two diseases, it appears to the writers unwise yet to regard the behavior of one as indicating exactly what that of the other will be, at least in commercial fields. Each variety of potato commonly grown in Maine apparently differs in susceptibility both in regard to the two diseases and in comparison with the other

[1] Such isolation or synthesis apparently will be necessary before it will be decided whether the convenient term "virus" represents an ultramicroscopic organism or an enzym. The two sides of the controversy are represented by Allard (*1, 2*) and Chapman (*5*).

varieties respecting either disease. The Irish Cobbler is the only one which in commercial fields often shows more than a trace of leafroll in northeastern Maine, and it seldom shows more than a trace of mosaic, while the Green Mountain and Bliss Triumph varieties are seldom found with only a trace of mosaic.

RELATION OF LEAFROLL TO CLIMATE

The Bliss Triumph variety contracts leafroll readily on Long Island and in Bermuda, in contrast to its behavior in northeastern Maine (*24*). This and similar differences between other geographical regions in regard to the rapidity of the spread of leafroll have been attributed to climatic differences. The question also arises whether or not greater prevalence of sources of infection, the importance of which is suggested by Murphy and Wortley (*14*), may be the chief or only cause of more rapid increase of leafroll in some regions within any given variety. As far as is now known, the greater prevalence of sources of infection on Long Island or Bermuda may now be the more important factor in the greater spread of leafroll there, with greater abundance of aphids helping both now and in the past to increase sources of infection. Climate, in turn, may differ enough to influence the abundance of aphids. In Virginia they are abundant in the winter (*21*) when entirely absent in Maine, except in the egg stage; and it seems probable that in sections intermediate as to climate their season begins earlier than in Maine and that they have greater opportunity to become numerous upon potatoes and to spread leafroll.

Whether or not the relative abundance of aphids is an important factor can be tested best by experiments in which parts of the same stock are grown at two or more places with surrounding conditions similar in regard to leafroll. The prevalence-of-source explanation is not necessarily supported by the less rapid spread of leafroll in Maine, as compared with that of mosaic, from diseased plants to those near by. It is possible that more severe inoculation by aphids is required to transmit leafroll than to transmit mosaic, and that these insects are abundant enough on Long Island and Bermuda to spread both diseases readily, but usually not in Maine. Inoculation of bruised leaves with virulent juice has proved far easier with mosaic than with leafroll. Aphids when introduced artificially have transmitted leafroll within the Green Mountain variety about as readily as they have mosaic (p. 59 and Table III). On the other hand, natural field inoculation by aphids in northeastern Maine evidently would be greater, even for mosaic, if there were more aphids. Hill selections made for freedom from mosaic in partly diseased fields in the valley of the St. John River in Maine ordinarily have given more satisfactory results than those made in the same manner in fields near Presque Isle, in correlation with less prevalence of aphids as indicated by counts made on leaves taken at random at the same time of year. Also, the number of aphids in Maine ordinarily is small enough for interseasonal

variation to have a marked influence upon the spread of mosaic (*19, p. 331*).

Reduction of the spread of leafroll by shade, in comparison with the spread in drouth conditions, has been reported by Wortley (*24, p. 519*). It seems possible that aphids might be more restless and inclined to disperse from plant to plant in drouth conditions and that their dispersal might be reduced in shade conditions by a fungous disease. Such a disease has been noted in Maine by the writers as being more prevalent in insect cages than in the open field during sunny weather and as practically eradicating an abundant infestation within a few days of cloudy weather. It may be suggested that the normal weather conditions of northeastern Maine specially favor any fungous disease of aphids, even as they favor the growth of the potato plant and the development of its important malady, the late blight (*Phytophthora infestans* de By).

CONTROL OF LEAFROLL

Roguing tests were begun in 1919 in order to ascertain whether or not it was possible to free infected potato stock from leafroll plants. Two stocks, lots 20 and 21 of Table XIII, have been grown upon the experimental plots in northeastern Maine since 1916. They were at first a single healthy stock which did not yet contain any leafroll plants in 1918 when it was divided and located in two rows next to a 100 per cent leafroll row. It was exposed to heavy aphid infestation in 1918, and in 1919 it developed leafroll in 5 per cent of the plants from one row and in 11 per cent of those from the other. In 1919 a part (sublot 1) of each of these 1-row lots was rogued, while another part (sublot 2) was not rogued. That season these lots were again located, as indicated, near or next to wholly leafroll stock, and numerous aphids, though not so many as in 1918, appeared during the latter part of the season. At harvesting time only tubers of approximately 4 ounces and more were selected.

Lot 22 as noted was taken from a commercial field having 14 per cent leafroll infection. This field is located fully half a mile from the experimental plots on which lots 20 and 21 were grown. It happened that aphids were very scarce there, only a few individuals to a plant being noted late in the season. Part of this stock was rogued and designated as sublot 1, while sublot 2 of this same stock was not rogued. The selection of tubers was the same as for lots 20 and 21. Observations on these lots are reported in Table XIII.

In view of the varying conditions obtaining in connection with the different lots described in Table XIII, it will be impossible to consider that a single factor caused the differences in leafroll percentages in 1920. Apparently selecting tubers in 1919 reduced the leafroll percentage in the unrogued sublots of lots 1919–21 and 1919–22, while such an effect was prevented in lot 1919–20 by greater proximity to a leafroll row. In sublot 1 of lot 1919–20 roguing prevented an increase in leafroll per-

centage which resulted in sublot 2, in spite of tuber selection, from proximity to a source of virulent aphids. In sublot 1 of lot 1919–21 roguing produced a greater reduction in leafroll than in sublot 1 of lot 1919–20, apparently because of a greater distance from entirely leafroll stock.

TABLE XIII.—*Effect of roguing upon percentage of leafroll*

Lot No.[a]	Variety.	First season.				Second season.	
		Location.	Percentage of leafroll.	Sublot No.	Roguings.	Total number of hills.	Percentage of hills leafroll.
1918–4	Bliss Triumph.	Aroostook Farm plant-disease plot, two rows.	(b)	1	1	1,332	2
				2	0	1,615	8
1919–15	Green Mountain.	Aroostook Farm plant-disease plot, one row.	5	1	1	1,641	0.2
				2	0	1,489	4
1919–20	Irish Cobbler.	Aroostook Farm next all-leafroll row.	5	1	2	1,254	4.7
				2	0	954	10
1919–21	...do.....	Aroostook Farm third row from all-leafroll row.	11	1	2	1,321	.5
				2	0	954	3.8
1919–22	...do.....	Commercial field.....	14	1	1	639	0
				2	0	637	8

[a] The year of planting (first season) is given as part of the lot number.
[b] Rogued so late (August 16) that hot weather and age caused many undoubtedly healthy hills to look as if possibly leafroll.

It is noteworthy that in lots 15 and 22 leafroll was entirely eliminated from sublot 1 by a single roguing. The marked reduction of leafroll in sublot 2 of lot 22 apparently was due to a large percentage of the leafroll vines producing tubers weighing less than 2 ounces and to the selection of large tubers together with the scarcity of aphids in this field. Hence it appears that leafroll may be eliminated from infected stock by roguing, provided that such stock is not in close proximity to leafroll vines infested with aphids, and may be reduced by discarding small tubers. This means that in northeastern Maine leafroll may be controlled more readily than mosaic of potato (*19, p. 270*). Whether this is due to less prevalence of diseased plants or to less susceptibility under the existing conditions of aphid infestation remains to be determined by further investigation. In either case it would not be advisable to expect similar results elsewhere where either diseased plants or aphids are more numerous.

From the data on hill selections (p. 53) it is apparent that this method of selection does not necessarily insure stock free from leafroll if such selection is practiced near leafroll plants infested with aphids. Hence, in view of the fact that elimination of leafroll hills from the seed plot by roguing appears to be fully as effective as hill selection, the former method of eradication seems the more desirable one. From the results on aphid transmission it is very evident that the earlier the diseased plants are

removed from the seed plot the less chance there will be for infection from such plants. This is more particularly the case in those sections of the country where aphids become very numerous relatively late in the development of the vines. Furthermore, isolation of the seed plot from diseased plants in adjoining plots or fields also will contribute to the effectiveness of roguing.

SUMMARY

(1) Potato leafroll of the apparently nonparasitic transmissible type, also called phloem-necrosis, is probably as widely distributed over the earth as are potatoes. Its exact geographical distribution is difficult to ascertain, however, because of the present impossibility of easily identifying it by the isolation of a pathogene or other cause and because of the resulting tendency to apply the name to unrelated diseases with somewhat similar symptoms. The same may be said of net-necrosis and spindling-sprout.

(2) The chief and perhaps the only manner of transmission from season to season in the soil or elsewhere is by means of tubers from diseased plants.

(3) Leafroll usually reduces the yield considerably, and, inasmuch as it is inheritable, it decreases the value of the tubers for seed. It may also lessen the value of the tubers for other purposes.

(4) Leafroll is transmissible from one plant to another by means of grafting either tubers or stalks and by means of aphids.

(5) Net-necrosis is apparently a leafroll symptom, being a discoloration which results from tuber phloem-necrosis and which appears more often as conditions of variety, recency of infection, and weight of tuber are more favorable. It develops in the dormant tubers without relation to differences in the storage temperature. When it occurs as a symptom of leafroll, the effects of the latter are still more detrimental, one being a decided spindliness of the sprouts. Transmission and control of leafroll are thus concerned indirectly with net-necrosis and spindling-sprout.

(6) Leafroll and mosaic are somewhat similar types of diseases.

(7) Inter-regional differences in the spread of leafroll may depend upon differences in climate and in the abundance of aphids.

(8) Roguing has proved to be much more effective in eliminating leafroll than it has been for mosaic, at least in northeastern Maine.

LITERATURE CITED

(1) ALLARD, H. A.
1915. EFFECT OF DILUTION UPON THE INFECTIVITY OF THE VIRUS OF THE MOSAIC DISEASE OF TOBACCO. *In* Jour. Agr. Research, v. 3, no. 4, p. 295–299

(2) ———
1916. SOME PROPERTIES OF THE VIRUS OF THE MOSAIC DISEASE OF TOBACCO. *In* Jour. Agr. Research, v. 6, no. 17, p. 649–674, pl. 91. Literature cited, p. 673–674.

(3) APPEL, Otto.
1915. LEAF ROLL DISEASES OF THE POTATO. *In* Phytopathology, v. 5, p. 139–148.

(4) BARTHOLOMEW, E. T.
1915. A PATHOLOGICAL AND PHYSIOLOGICAL STUDY OF THE BLACK HEART OF POTATO TUBERS. *In* Centbl. Bakt. [etc.] Abt. 2, Bd. 43, No. 19/24, p. 609–639, 3 pl. Literature cited, p. 637–638.

(5) CHAPMAN, G. H.
1917. MOSAIC DISEASE OF TOBACCO. Mass. Agr. Exp. Sta. Bul. 175, p. 73–117, 5 pl.

(6) COOK, Mel T.
1919. POTATO DISEASES IN NEW JERSEY. N. J. Agr. Exp. Sta. Circ. 105, 38 p., 19 fig.

(7) COONS, G. H.
1918. MICHIGAN POTATO DISEASES. Mich. Agr. Exp. Sta. Spec. Bul. 85, 49 p., 41 fig.

(8) DOBY, G.
1911. BIOCHEMISCHE UNTERSUCHUNGEN ÜBER DIE BLATTROLLKRANKHEIT DER KARTOFFEL. II. DIE OXYDASEN DER RUHENDEN UND ANGETRIEBENEN KNOLLEN. *In* Ztschr. Pflanzenkrank., Bd. 21, Heft 6, p. 321–336, illus.

(9) GÜSSOW, H. T.
1916. REPORT FROM THE DIVISION OF BOTANY. . . . 1914/15. *In* Canada Exp. Farms Rpt. 1914/15, p. 949–990, 2 fig., pl. 63–73.

(10) HASKELL, Royal J.
1919. FUSARIUM WILT OF POTATO IN THE HUDSON RIVER VALLEY, NEW YORK. *In* Phytopathology, v. 9, no. 6, p. 223–260, pl. 13–15. Literature cited, p. 259–260.

11) ——— and MARTIN, G. H.
1919. SUMMARY OF PLANT DISEASES IN THE UNITED STATES IN 1918. II. DISEASES OF FIELD AND VEGETABLE CROPS. *In* U. S. Dept. Agr. Bur. Plant Indus. Plant Disease Bul. Supl. 2, p. 42–83.

(12) JONES, L. R., MILLER, M., and BAILEY, E.
1919. FROST NECROSIS OF POTATO TUBERS. Wis. Agr. Exp. Sta. Research Bul. 46, 46 p., 12 fig., 1 pl. (col.). Literature cited, p. 45–46.

(13) MURPHY, PAUL A., and WORTLEY, E. J.
1918. DETERMINATION OF THE FACTORS INDUCING LEAF ROLL OF POTATOES PARTICULARLY IN NORTHERN CLIMATES. FIRST PROGRESS REPORT. *In* Phytopathology, v. 8, no. 4, p. 150–154, 1 fig.

(14) ——— ———
1920. RELATION OF CLIMATE TO THE DEVELOPMENT AND CONTROL OF LEAF ROLL OF POTATO. *In* Phytopathology, v. 10, no. 9, p. 407–414, 1 fig. Literature cited, p. 414.

(15) ORTON, W. A.
1914. POTATO WILT, LEAF-ROLL, and RELATED DISEASES. U. S. Dept. Agr. Bul. 64, 48 p., 16 pl. Bibliography, p. 44–48.

(16) QUANJER, H. M.
1913. DIE NEKROSE DES PHLOËMS DER KARTOFFELPFLANZE, DIE URSACHE DER BLATTROLLKRANKHEIT. *In* Meded. Rijks Hoogere Land-, Tuin- en Boschbouwschool [Wageningen], deel 6, afl. 2, p. 41–80, pl. 2–9.

(17) ———
1920. THE MOSAIC DISEASE OF THE SOLANACEAE, ITS RELATION TO THE PHLOEM-NECROSIS, AND ITS EFFECT UPON POTATO CULTURE. *In* Phytopathology, v. 10, no. 1, p. 35–47, 14 fig. Literature cited, p. 47. (Essentially a reprint of the English summary, and of part of the figures and bibliography of (18) below.)

(18) QUANJER, H. M., et al.

1919. DE MOSAIEKZIEKTE VAN DE SOLANACEËN HARE VERWANTSCHAP MET DE PHLOEEMNECROSE EN HARE BETEEKENIS VOOR DE AARDAPPELCULTUUR. *In* Meded. Rijks Hoogere Land-, Tuin- en Boschbouwschool [Wageningen], deel 17, afl. 1/3, p. 1–90, 8 pl. (1–2 col.). Literatuur, p. 67–70. Summary [in English], p. 71–74.

(19) SCHULTZ, E. S., et al.

1919. INVESTIGATIONS ON THE MOSAIC DISEASE OF THE IRISH POTATO. *In* Jour. Agr. Research, v. 17, no. 6, p. 247–274, pl. A–B (col.), 25–30. Literature cited, p. 272–273.

(20) ——— and FOLSOM, Donald.

1920. TRANSMISSION OF THE MOSAIC DISEASE OF IRISH POTATOES. *In* Jour. Agr. Research, v. 19, no. 7, p. 315–338, pl. 49–56.

(21) SMITH, Loren B.

1919. POTATO SPRAYING EXPERIMENTS ON THE CONTROL OF THE PINK AND GREEN APHID (MACROSIPHUM SOLANIFOLII, ASHMEAD). PT. I. Va. Truck Exp. Sta. Bul. 29, p. 101–118, fig. 18.

(22) STEWART, F. C.

1916. OBSERVATIONS ON SOME DEGENERATE STRAINS OF POTATOES. N. Y. State Agr. Exp. Sta. Bul. 422, p. 319–357, 12 pl.

(23) ——— and SIRRINE, F. A.

1915. THE SPINDLING-SPROUT DISEASE OF POTATOES. N. Y. State Agr. Exp. Sta. Bul. 339, p. 133–143, 3 pl.

(24) WORTLEY, E. J.

1918. POTATO LEAF-ROLL: ITS DIAGNOSIS AND CAUSE. *In* Phytopathology, v. 8, no. 10, p. 507–529, 16 fig. Literature cited, p. 529.

PLATE 1

A.—Green Mountain potato plant, produced by a net-necrosis tuber and showing leafroll. For healthy plant in the same hill lot, produced by a healthy sister tuber see B.

B.—Healthy control to leafroll plant shown in A.

A

B

A

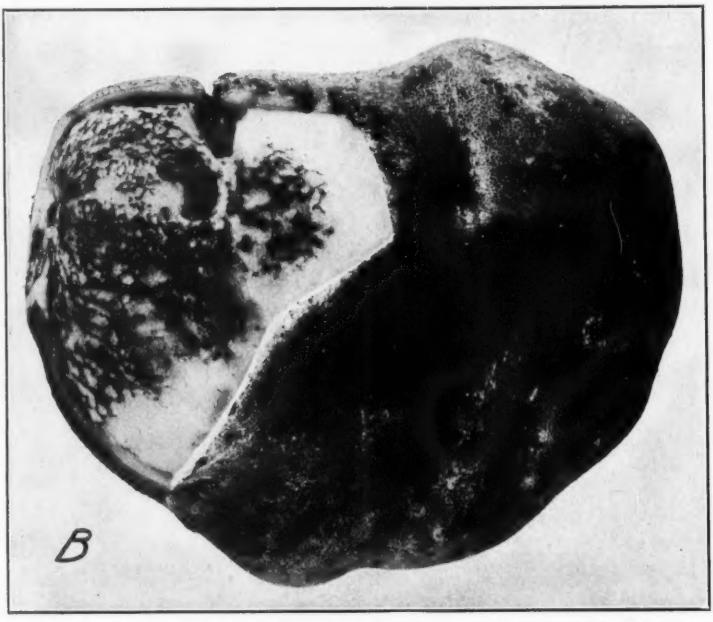

B

PLATE 2

A.—Greenhouse-grown progeny of a net-necrosis tuber from Green Mountain stock (lot 1919–125 of Table VI) showing net-necrosis and leafroll the preceding season.

B.—Tuber with part of stem end cut away to show net-necrosis. (From lot 1920–V of Table VI). The two deep holes are due to elimination of the effect of insect injury.

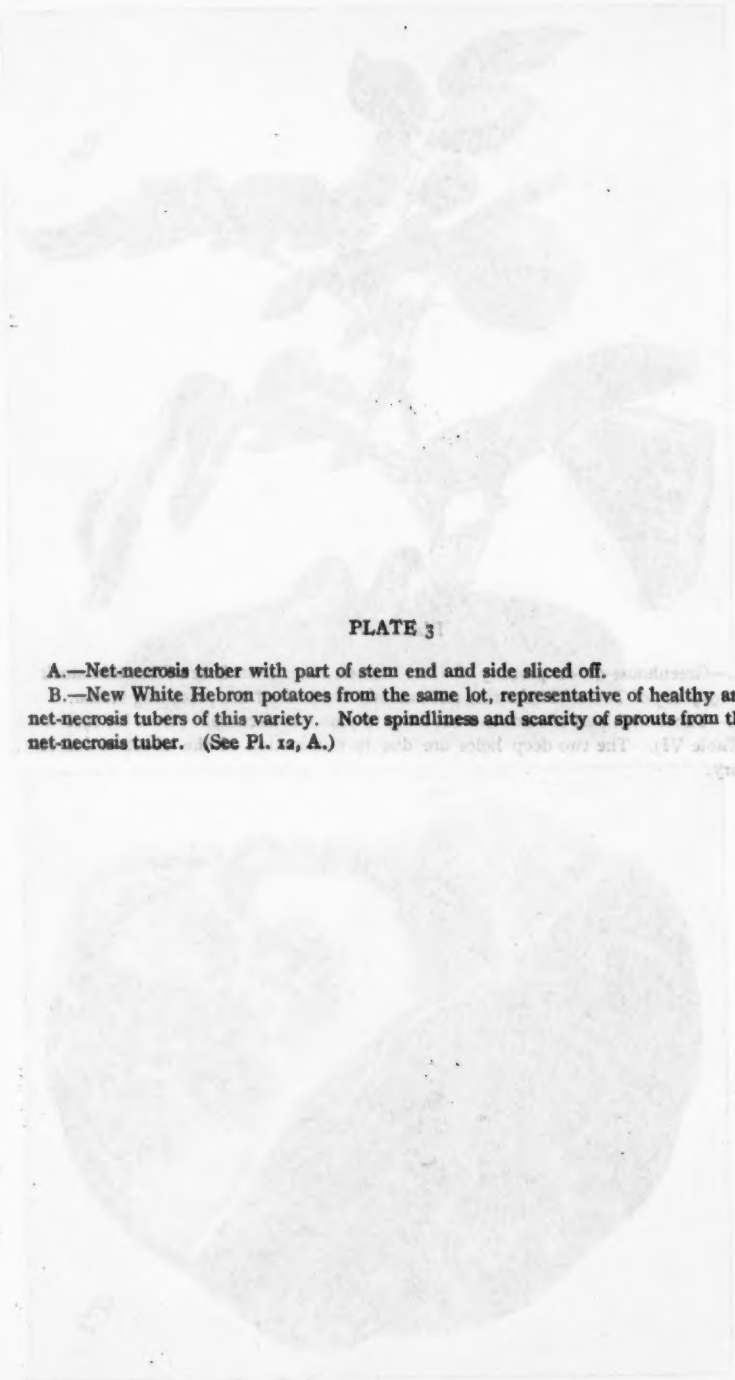
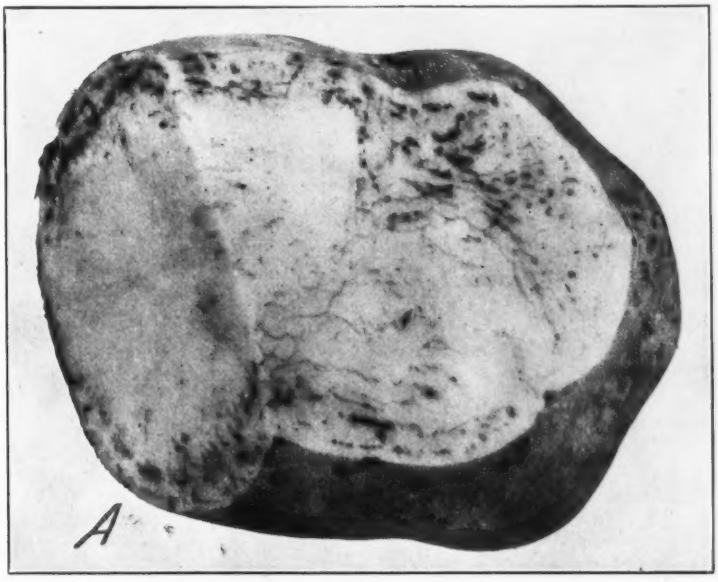
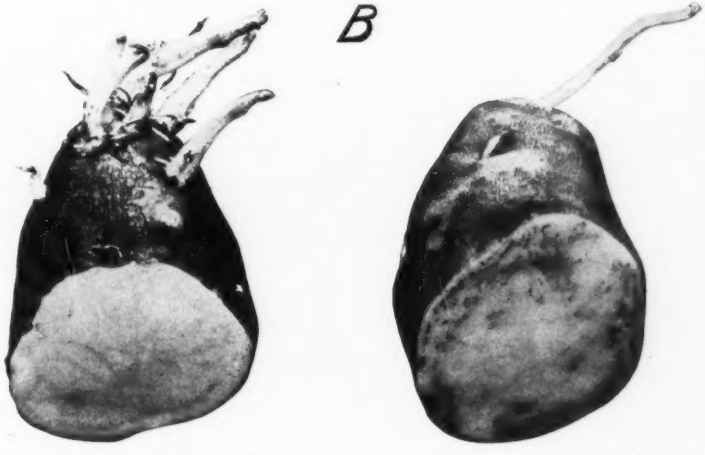


PLATE 3

A.—Net-necrosis tuber with part of stem end and side sliced off.

B.—New White Hebron potatoes from the same lot, representative of healthy and net-necrosis tubers of this variety. Note spindliness and scarcity of sprouts from the net-necrosis tuber. (See Pl. 12, A.)


A


B

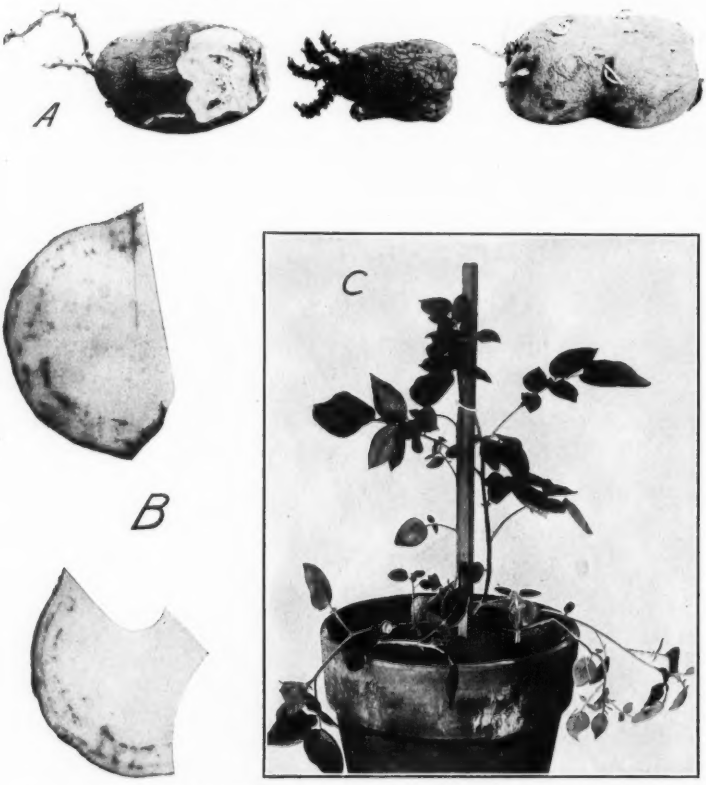

A
B
C

PLATE 4

A.—Green Mountain tubers kept in the same sack in a warm room from June 1 to August 11, 1919. The middle one had no net-necrosis and is withered, soft, and bearing normal sprouts. The others had net-necrosis and are smooth, firm, and bearing spindling sprouts.

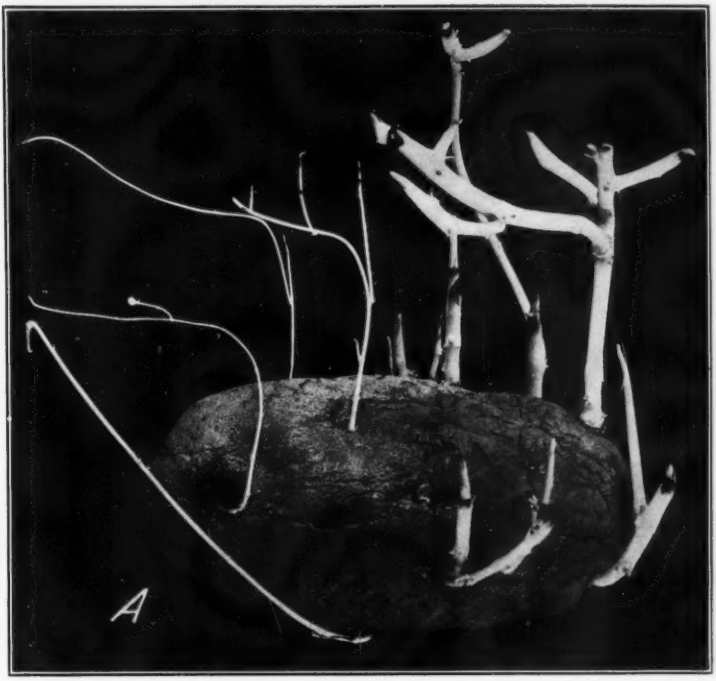
B.—Frost-necrosis of the net type produced by measured exposure to low temperature. Thin slices of Green Mountain tuber cut off to increase the visibility of the injury.

C.—Greenhouse-grown plant produced by a net-necrosis tuber (lot 1920–G of Table VI) and showing spindliness and slight leafroll.

PLATE 5

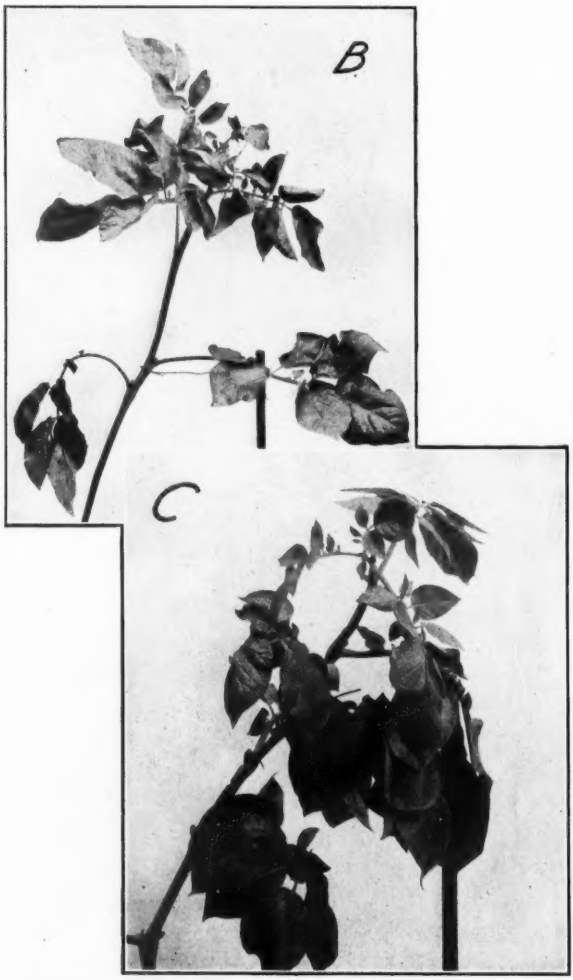
A.—Tuber with spindling sprouts coming from the part which later was found, by cutting, to be affected with net-necrosis.

B.—Two leafroll Green Mountain hills in the same hill lot, the one on the left produced by a half of a net-necrosis tuber and the one on the right produced by a half of a sister tuber that transmitted leafroll but showed no net-necrosis.


A

B

A


B
C

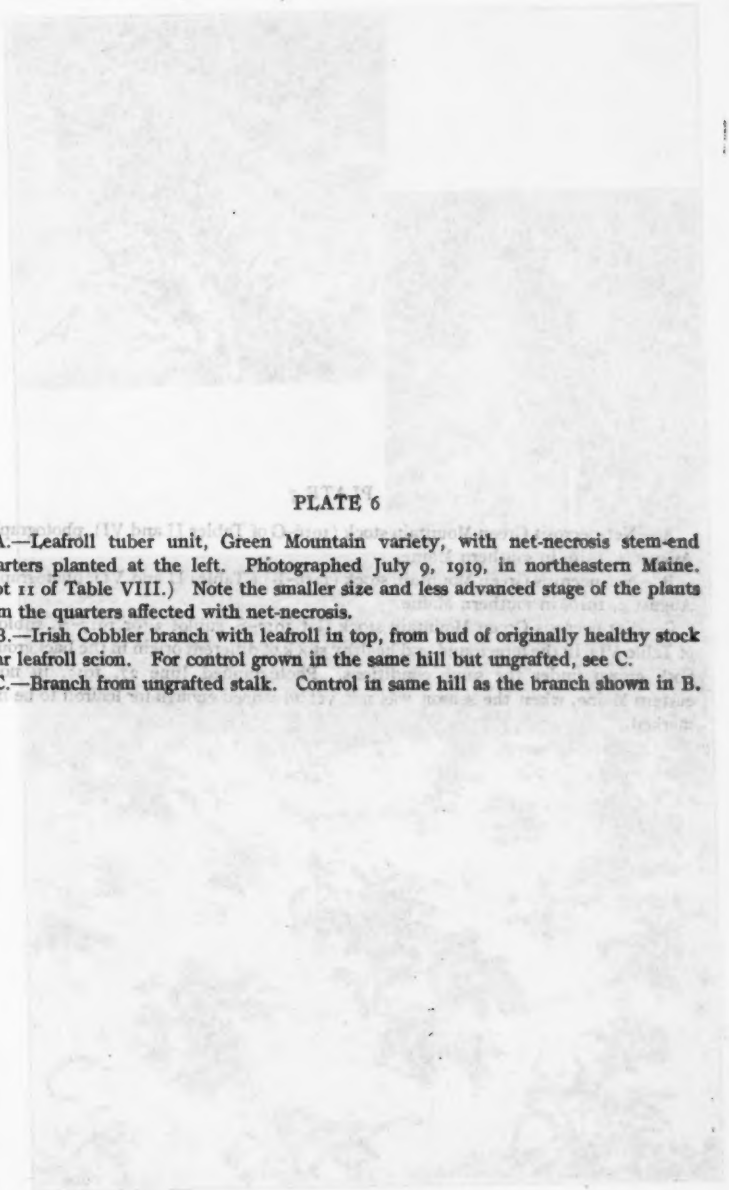


PLATE 6

A.—Leafroll tuber unit, Green Mountain variety, with net-necrosis stem-end quarters planted at the left. Photographed July 9, 1919, in northeastern Maine. (Lot 11 of Table VIII.) Note the smaller size and less advanced stage of the plants from the quarters affected with net-necrosis.

B.—Irish Cobbler branch with leafroll in top, from bud of originally healthy stock near leafroll scion. For control grown in the same hill but ungrafted, see C.

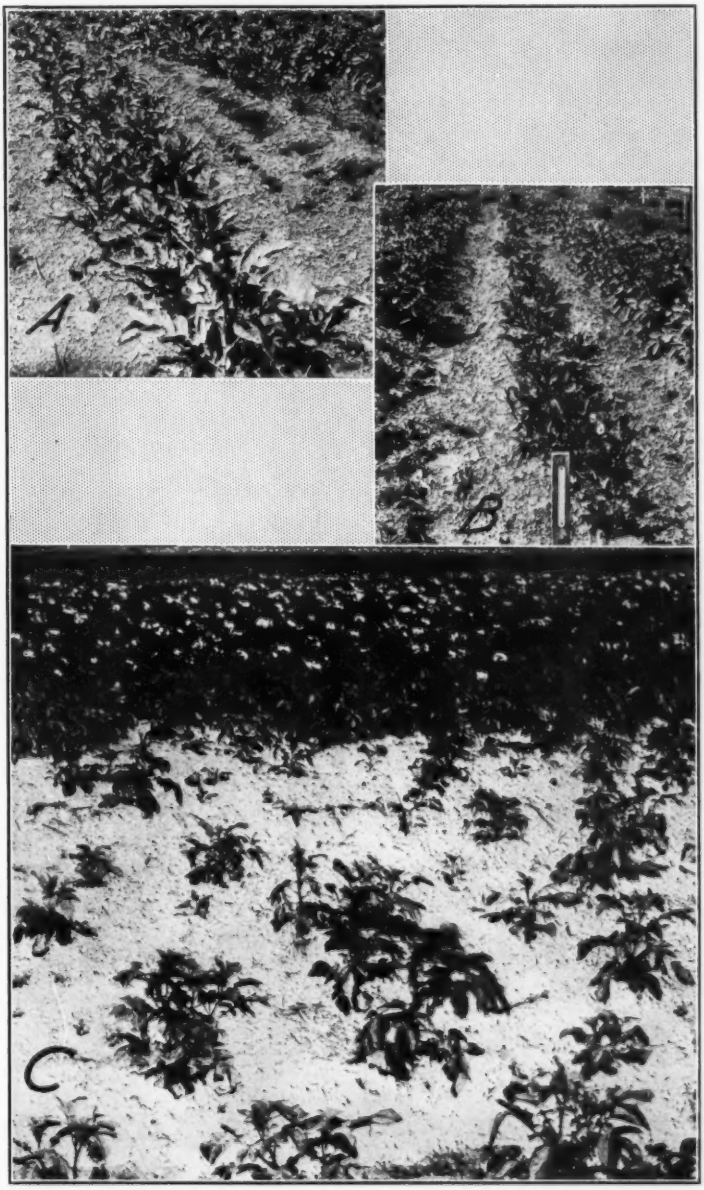
C.—Branch from ungrafted stalk. Control in same hill as the branch shown in B.

PLATE 7

A.—Net-necrosis Green Mountain stock (1916–G of Tables II and VI), photographed August 4, 1916, in southern Maine.

B.—Net-necrosis Green Mountain stock (1916–B of Tables II and VI), photographed August 4, 1916, in southern Maine.

C.—Net-necrosis Green Mountain stock (lot 1917–S, sublot 3, or 1917–A, sublot 3, of Table VI), in the foreground and healthy stock of different origin in the background, both grown under the same conditions. Photographed June 27, 1917, in northeastern Maine, when the season was not yet advanced enough for leafroll to be most marked.


A
B
C

A

B

PLATE 8

A.—Leafroll stalks from Irish Cobbler half tuber healthy when grafted upon leafroll half tuber. Removed from field to secure better photographic facilities and to ascertain absence of parasitic injury. For control, grown from other half of the same tuber, see B.

B.—Healthy control to plant shown in A.

PLATE 9

A.—Second-generation Green Mountain plant, leafroll as result of aphid inoculation of first generation in field insect cages. (See Table III.) For healthy control from the same stock, see B.

B.—Healthy control to plant shown in A.

A

B

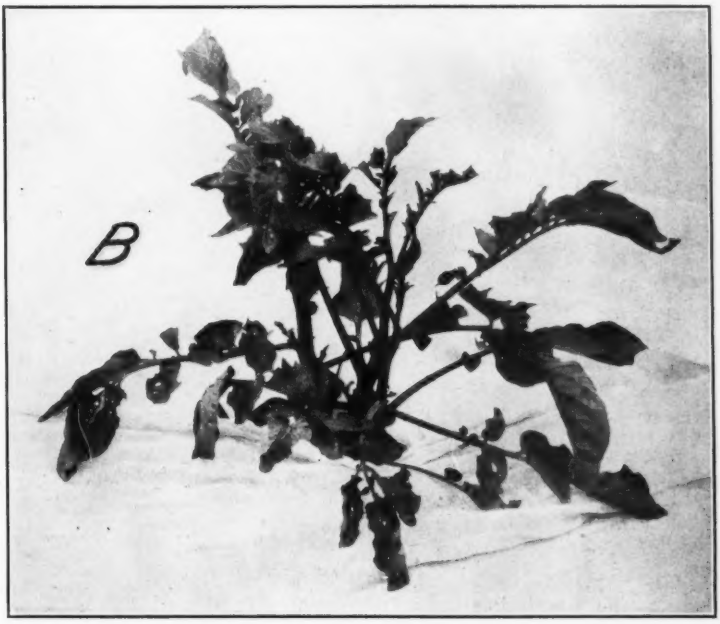
PLATE 10

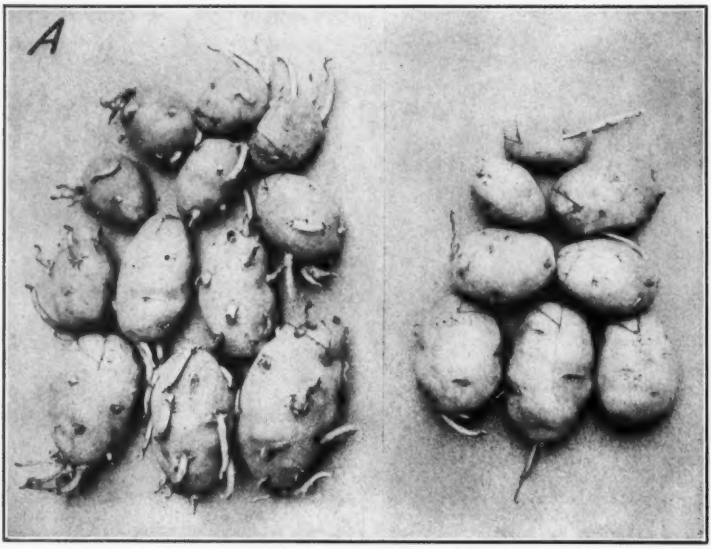
Irish Cobbler greenhouse-grown plants from halves of the same tuber. The one on the right has leafroll due to inoculation with aphids from a diseased plant. Its greater height is due to the seed piece having earlier sprouts. The control on the left was fed upon by aphids from mustard plants but remained healthy.

PLATE 11

A.—Second-generation progeny of uninoculated control shown in Plate 10,
B.—Second-generation progeny of inoculated stock shown in Plate 10.

A


B


A

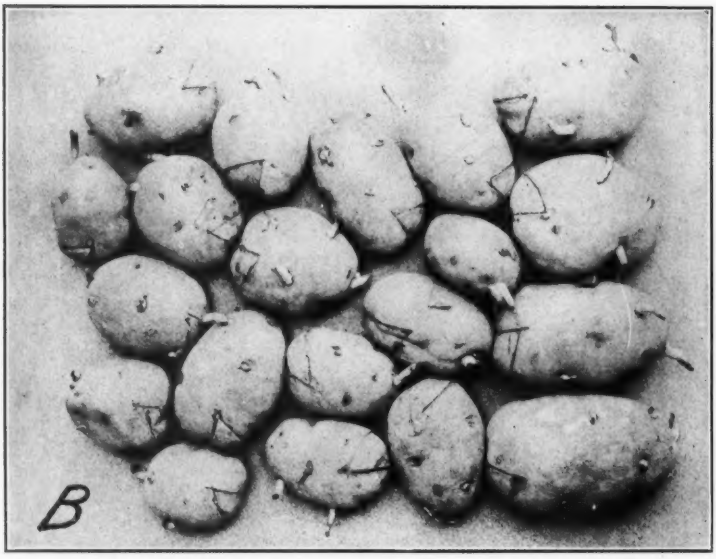

B

PLATE 12

A.—New White Hebron tubers from 1919 hills next to leafroll hills in the same row. (Half of lot V148, sublot 3, of Table VIII.) Examined for net-necrosis and photographed in the last week of May, 1920, in northeastern Maine. The group on the right showed net-necrosis, spindling-sprout, and reduction in the number of sprouts and produced leafroll plants. Representative tubers from the two groups are shown in section in Pl. 3, B. From same stock and row as tubers of Pl. 12, B.

B.—New White Hebron tubers from hills leafroll throughout 1919. (Lot V148, sublot 2, of Table VIII.) Examined and photographed in the last week of May, 1920, in northeastern Maine. From same stock and row as tubers of A, and like them showed suppression of sprouts, but in contrast showed no net-necrosis or spindliness.

GROWTH AND SAP CONCENTRATION[1]

By HOWARD S. REED,[2] *Professor of Plant Physiology, University of California*

Chandler (*1*)[3] found that trees making rapid growth had lower sap concentration and that slower growth of the tree was accompanied by higher concentration. Trees which made rapid growth as a result of severe pruning in the preceding winter had a lower concentration of sap than trees which had been lightly pruned. During the summer season the concentration of the cell sap was lowest near the ground and highest in the upper part of the tree. Although Chandler's method of preparing the samples for freezing-point determinations has been adversely criticized, one must acknowledge the advance he made in our knowledge of sap concentrations in fruit trees.

Dixon and Atkins (*3*) observed that the sap of young leaves of various plants had, as a rule, a lower osmotic pressure than sap from mature leaves.

Lutman (*10*) has determined the freezing-point depressions of the sap of the potato plant with reference to its growth cycles. The variations of concentration seem to be related to the development and rate of growth of the plant.

The seed tubers when taken from storage had a relatively high osmotic pressure, but as water was absorbed the osmotic pressure dropped. As the age of the plant increases its osmotic pressure increases on account of the accumulation of inorganic salts in its cells; but when senility begins, the osmotic pressure drops, because of the loss of soluble materials. In the young plant the leaf sap is more concentrated than the stalk sap, but after the flower buds are put out and the tubers begin to grow, the stalk sap is more concentrated. With the advent of cool, rainy weather later in the season the leaves begin to grow again and their sap concentration is greater than that of the stalks. Shading the potato plant diminishes the osmotic pressure of the leaves and stalk.

Synopses of the earlier literature dealing with cryoscopic methods and with the relation of the physical environment to the concentration of the cell sap will be found in the summaries prepared by Dixon (*2*), Hibbard and Harrington (*7*), and Harris and Lawrence (*5*).

---

[1] Paper No. 71, University of California, Graduate School of Tropical Agriculture and Citrus Experiment station, Riverside, Calif.

[2] It is a pleasure to acknowledge the aid which has been rendered by those associated with the progress of this work. The author's thanks are due to Messrs. L. C. Masters, R. H. Holland, and F. F. Halma.

[3] Reference is made by number (italic) to "Literature cited," p. 98.

METHODS OF EXPERIMENT

The methods of preparing and examining the material have been adapted to the needs of the work here reported. As the work of making several hundred determinations progressed, a routine procedure was followed which stabilized, if it did not remove, the sources of error. The chief object of this work has been to study comparative concentration of sap as related to the growth rate. The results obtained, though not free from error, are comparable with each other and give a satisfactory picture of an important physiological relation.

The plant material was collected in the field and packed at once in a tight container. For small samples, the container was a quart fruit jar with a screw top. For large samples, especially constructed steel cylinders, 6 inches in diameter by 14 inch tall, were used. The open end of the cylinder was provided with an accurately fitting metal cap and rubber gasket. The cap could be drawn down tightly on the rubber gasket by means of three bolts, and the cylinder was thus effectively sealed.

The samples were always collected between 9 and 10 o'clock in the forenoon, in order to avoid the possibility of diurnal fluctuations in concentration. As soon as filled, the containers were brought to the laboratory and packed in an ice-salt mixture for the preliminary freezing which killed the protoplasm and increased the permeability of the material. The supply of ice and salt was renewed as occasion required. The containers remained in this mixture for 18 to 24 hours, to insure complete freezing of the material. When the containers were removed they were washed to remove all adhering brine and wiped dry. The material was removed and ground in a small hand mill and then pressed in a strong screw press. Not more than 20 minutes were required to grind a sample and express the sap. The mill and press were heavily tinned, and there was no apparent corrosive action of the plant juices on any part of them after continued use.

The expressed sap was received in small bottles which were closed with rubber stoppers and placed on ice, in case the sap was not to be immediately used. Samples which had stood for more than two or three hours were discarded. In spite of these precautions, there was some oxidation of the plant saps and probable change in concentration; but the error, if any, due to such changes was shared to approximately the same extent by all samples and is not believed to vitiate the results.

The freezing point of the sap was determined in the usual freezing apparatus with the use of a Beckmann thermometer. At least two determinations were made upon each sample, and the average of closely agreeing duplicates was taken as the freezing point. The osmotic pressures were calculated by the method given by Harris and Gortner (*4*).

The rate of growth of the trees was obtained by measuring the length of certain selected shoots at intervals of seven days. Each shoot bore a

numbered tag and was marked near the base with a line of India ink. The distance from the basal ink mark to the tip of the shoot was easily determined and recorded for each shoot.

GROWTH INCREMENTS AND SAP CONCENTRATION OF YOUNG WALNUT TREES

Determinations on the concentration of the cell sap of young walnut trees (*Juglans* spp.) were made at frequent intervals and compared with the increments in mean height of similar trees growing in the same rows. The measurements given in Table I were made upon a population of *J. regia* trees, of which the majority were propagated upon *J. nigra* rootstocks and the remainder on a variety of *J. regia* known as "Hardshell." The trees from which the material for investigation was taken were in their second season's growth. They stood in the nursery row in a fertile soil and were artificially irrigated. The first samples for determinations were taken June 8 and the last on November 12.

The growth rate of a portion of this group of walnut trees has been discussed in a recent publication (*12*) and has been shown to follow the course of autocatalytic reactions.

TABLE I.—*Mean growth increments and concentration of cell sap of walnut trees*

Date.	Mean height.	Increment of growth during preceding week.	Osmotic pressure of cell sap.
	Cm.	*Cm.*	*Atmospheres.*
June 12	62.6	12.6	16.5
19	66.6	4.0	13.5
26	73.7	7.1	18.4
July 4	87.2	13.5	9.7
11	100 8	13.6	11.4
23	125.9	[b] 15.0	10.4
30	136.7	10.8	10.8
Aug. 6	147.6	10.9	.....
13	153.4	5.8	17.8
20	[a] 160.9	[a] 7.5	.....
27	168.4	[a] 7.5	12.5
Sept. 4	176.7	8.3	9.2
10	184.2	[b] 8.7	8.9
17	188.1	3.9	10.2
24	191.3	3.2	18.8
Oct. 1	194.6	3.3	11.7
8	196.8	2.2	20.9
15	199.0	2.2	13.2
22	199.7	0.7	17.1
29	201.2	1.5	13.5
Nov. 5	201.2	0.0	24.4

[a] Interpolated values. [b] Calculated to 7-day basis.

The samples collected for freezing-point determinations always consisted of the total growth of a shoot of that particular season (*ab initio*) and included both stems and leaves. Toward the end of the growing season the stems were large and woody; nevertheless they were ground in the handmill and pressed like the other material. Most of the sap so obtained came undoubtedly from the cortical layers of the stems.

By referring to Table I the reader will see the nature of the results obtained in this work. The table shows the mean height of the trees (from the basal ink mark), the height increment from the preceding measurement, and the concentration of the cell sap expressed in atmospheres of osmotic pressure. The mean height increased from 62 cm. on June 12 to 201.2 cm. on October 29. The increments (calculated in each case to a 7-day basis) were far from uniform, ranging as they do from 0.7 cm. to 15 cm. The atmospheres of osmotic pressure of expressed

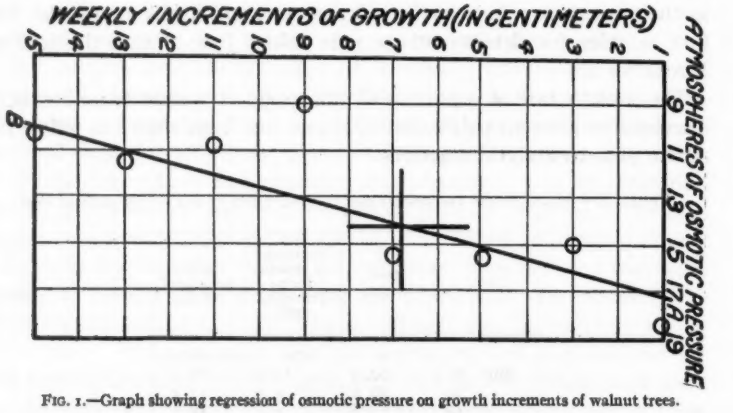


FIG. 1.—Graph showing regression of osmotic pressure on growth increments of walnut trees.

sap range from 8.9 to 24.4. Thus it will be seen that there are periodic variations in the concentration of the cell sap and in the growth rate from week to week during the season. The maximum growth rate was observed during certain weeks in July, and the maximum osmotic pressure of the cell sap was observed near the end of the growing season.

It is somewhat difficult to get a comprehensive idea of the relationship between growth and sap concentration from the array of figures given in Table I. It will be better to investigate the nature and amount of the mathematical correlation between the two sets of values. There are 19 observations in which both the increments and sap concentration were determined. While this number is rather scanty for determining correlation, the regression is remarkably linear (fig. 1), and it is believed that the correlation coefficient is trustworthy. The coefficient of correlation between the two variables is -0.557 ± 0.113. The negative

correlation shows that when growth is rapid the sap concentration is lower and when growth is slower the sap concentration is higher.

These conclusions may be verified by inspection of the figures in Table I. For example, an increment of 15 cm. in the week ending July 23 coincided with a sap concentration of 10.4 atmospheres, while smaller increments coincided usually with higher sap concentrations. The small growth increments in the latter part of the season are accompanied by the highest concentrations of plant sap. The concentration of solutes in the sap tends to increase with age of the leaf, as Dixon and Atkins (*3*) discovered in the study of Ilex.

GROWTH INCREMENTS AND SAP CONCENTRATION OF YOUNG APRICOT TREES (1918)

The question of sap concentration in shoots of young apricot trees in relation to growth was also investigated. The trees from which the material was obtained had been growing in the orchard two years when these studies were started. Soon after the season's growth began, 70 young shoots were selected and marked with labels. An India ink mark was made near the base of each shoot, from which length measurements were made at intervals of seven days. At the time of making the measurements here recorded a sample of shoots was collected from adjacent trees, and these samples were used for determining the sap concentration. The samples consisted of entire shoots of that particular season's growth. The stems and leaves were ground together, and the sap was expressed. The samples were given a preliminary freezing and were treated essentially as the walnut samples were treated.

The growth and sap concentration determinations made in 1918 upon apricot shoots are given in Table II. It will be noted that where the intervals were not exactly seven days the increments were calculated to a 7-day basis in order to make them comparable. It will be noted that the rate of growth was greatest at the outset of the observations and diminished with several fluctuations to the end of the growing season. Certain dynamical aspects of this growth rate have been discussed in a separate paper (*11*) though the studies there related were based upon another set of measurements.

The concentration of the cell sap (expressed in atmospheres of osmotic pressure), although subject to some fluctuation, increased as the season advanced. The lowest concentration was observed on May 21 and the highest on October 31. The average osmotic pressure, expressed in atmospheres by months, is: May, 11.84; June, 13.66; July, 14.34; August, 15.04; September, 15.18; October, 16.48. Table II shows that the concentration of the sap, which was 12.71 atmospheres on May 2, fell to 10.87 in the next three weeks, simultaneously with rapid elongation of the shoots. The concentration at once began to rise and went up, with some irregularities, to 18.90 atmospheres on October 31.

TABLE II.—*Mean growth increments of shoots and concentration of sap of apricot trees (1918)*

Date.		Mean length.	Increment of growth during preceding week.	Osmotic pressure of cell sap.
		Cm.	*Cm.*	*Atmospheres.*
May	2	45.0	19.0	12.71
	8	60.6	[b] 18.2	11.68
	15	74.1	13.5	11.99
	21	83.9	[b] 11.4	10.87
	29	92.4	[b] 7.4	11.95
June	7	103.9	[b] 9.0	12.30
	12	105.9	[b] 2.8	14.96
	19	108.5	2.6	13.52
	26	113.0	4.5	13.86
July	3	122.6	[b] 8.4	13.66
	10	134.2	11.6	14.24
	17	143.3	9.1	16.05
	24	148.0	4.7	15.28
	31	155.1	7.1	12.47
Aug.	7	162.2	7.1	14.87
	14	167.4	5.2	14.88
	21	170.0	2.6	15.17
	28	173.9	3.9	15.28
Sept.	5	[a] 184.2	[b] 9.1	15.54
	12	189.3	5.1	16.42
	19	192.3	3.0	13.46
	26	196.7	4.4	15.30
Oct.	3	199.3	2.6	15.64
	9	201.0	[b] 2.0	14.52
	16	203.2	2.2	14.99
	23	204.6	1.4	18.36
	31	206.8	[b] 1.9	18.90
Nov.	6	207.3	.5	17.66

[a] Interpolated value. [b] Calculated to 7-day basis.

The degree of association between the amount of growth in a week and the concentration of the cell sap at the end of that week is more succinctly expressed by the coefficient of correlation, which was found to be

$$r = -0.613 \pm 0.079.$$

This coefficient is of sufficient magnitude to express a strong negative correlation between growth and sap concentration. The regression of the two variables is approximately linear (fig. 2), though there is a marked tendency for the points to scatter. These determinations are based on 28 observations, however, and are regarded as somewhat more reliable than those for the walnut trees.

These observations, made at frequent intervals throughout a growing season, show that rapid growth is marked by a lower sap concentration and vice versa. In material of this kind, the concentration of the cell sap is probably due mostly to sugars and other organic compounds.

EFFECT OF PRUNING UPON SAP CONCENTRATION

The results obtained from determinations on the walnut and apricot trees are interesting and seem conclusive so far as they go, but they raise other questions which seem worthy of study.

In pursuance of these inquiries, determinations were made on the same block of apricot trees throughout the season of 1919. The growth and sap concentration were determined on two lots of trees, one of which is heavily pruned each winter while the other is not pruned at all. Needless to say, the growth of individual shoots on the heavily pruned tree, was much greater than that of shoots on the unpruned trees.

The mean length of shoots was determined at weekly intervals, as before. In the beginning, 50 shoots were selected on each lot of trees,

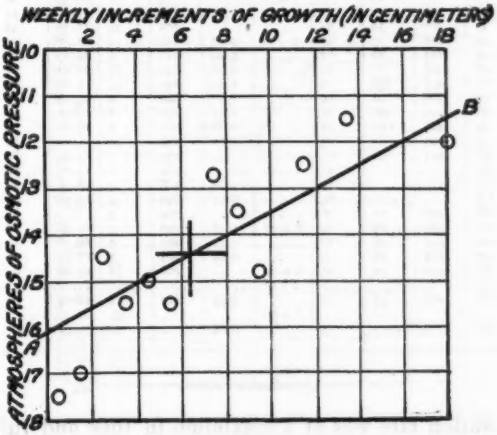


FIG. 2.—Graph showing regression of osmotic pressure on growth increments of apricot trees (1918).

but, as a result of breakage and other accidents, a number had to be eliminated. The computations are based on 33 shoots on the unpruned trees and on 28 shoots on the heavily pruned trees. The evaporating power of the air was determined by the evaporation of distilled water from a white, spherical atmometer bulb supported on a stand 5 feet from the ground in the center of the orchard. The average daily temperature was taken from the Riverside official reports, which were obtained from standard instruments located about 2 miles distant. The soil moisture was determined from composite samples taken to a depth of 3 feet throughout the area occupied by the trees in question. The sap concentration was determined by the depression of the freezing point.

A summary of the several factors is shown in Table III.

TABLE III.—*Growth and sap concentration of pruned and unpruned apricot trees (1919), with comparison of three environmental factors*

Date.	Time.	Evaporation.		Mean daily temperature.	Water added.[a]	Soil moisture.	Shoots on pruned trees.			Shoots on unpruned trees.		
		Per week.	Per day.				Mean length.	Increment of growth during preceding week.	Osmotic pressure.	Mean length.	Increment of growth during preceding week.	Osmotic pressure.
	Days.	*Cc.*	*Cc.*	*° F.*	*Acre-inches.*	*Per cent.*	*Cm.*	*Cm.*	*Atmospheres.*	*Cm.*	*Cm.*	*Atmospheres.*
Apr. 9	.....	.....	.....	.....	.....	.....	13	.....	.....	9	.....	.....
16	7	350	50	62	.....	.....	37	24	13.82	17	8	14.49
23	14	427	61	64	.....	.....	60	23	13.52	25	8	13.61
30	21	185	26	57	r 0.82	.....	73	13	11.72	29	4	13.41
May 7	28	192	27	61	i 3.40	.....	88	15	11.00	34	5	14.52
14	35	267	38	65	.....	.....	102	14	11.38	42	8	13.90
21	42	246	35	65	r .72	9.18	113	11	11.60	50	8	15.19
28	49	155	22	67	.....	9.43	121	8	12.75	57	7	13.97
June 4	56	508	72	73	.....	8.56	132	11	13.01	63	6	14.57
11	63	455	65	72	.....	8.39	142	10	13.82	68	5	16.73
17	69	366	61	69	.....	8.17	148	6	15.27	71	3	17.43
25	77	808	101	81	.....	7.53	156	8	14.76	77	6	15.94
July 2	84	447	64	73	.....	6.78	163	7	16.60	79	2	17.88
9	91	595	85	75	.....	5.60	174	11	.....	82	3	.....
16	98	501	72	78	.....	.....	177	3	15.87	83	1	19.77
23	105	.....	.....	75	i 2.70	.....	182	5	15.77	84	1	20.96
30	112	.....	.....	79	.....	7.22	186	4	18.51	85	1	21.81
Aug. 6	119	.....	.....	69	.....	6.02	190	4	14.09	86	1	17.14
13	126	496	71	76	.....	.....	194	4	.....	87	1	.....
20	133	483	69	79	i 2.81	5.48	197	3	16.38	88	1	19.50
27	140	334	48	77	.....	7.52	200	3	18.58	89	1	22.04
Sept. 3	147	263	38	74	.....	6.05	203	3	17.03	90	1	16.16
24	168	350	50	74	i 2.62	.....	208	2	19.66	94	1	21.94
Oct. 1	175	.....	.....	.....	r 1.37	.....	.....	.....	.....	.....	.....	.....
8	182	260	37	72	.....	5.92	210	1	22.73	94	0	19.40
13	.....	.....	.....	.....	i 3.80	.....	.....	.....	.....	.....	.....	.....
21	195	.....	.....	73	.....	6.66	.....	.....	.....	.....	.....	.....

[a] r= rain.
i= irrigation water.

The evaporation rate was at a maximum in June and July. During May the prevailing weather was cloudy, and the evaporation rate was thereby diminished. The mean monthly temperatures were as follows: April, 61° F.; May, 65°; June, 74°; July, 76°; August, 75°; and September, 74°.

The soil moisture diminished in quantity as the season advanced, in spite of the irrigations. The June irrigation was omitted on account of the ripening fruit. The figures show how the moisture content of the soil rose after each application of water.

The growth of the selected shoots on the pruned and on the unpruned trees was most rapid in the early part of the season. There were more or less distinct cycles of growth in each case, though they were more evident in the case of the heavily pruned trees. The increments in mean length are reduced to a 7-day basis. The mean growing season was approximately the same for each class of shoots, although the rate of growth of the unpruned shoots was very slow after the middle of July. Certain

dynamical features of the growth rate of these trees have been described in another paper (*13*) and will not be discussed here.

The concentration of the cell sap of the two classes of shoots fell off somewhat after the observations were started, then rose, although fluctuating, toward the end of the growing season. The concentration of the sap of the slower shoots on the unpruned trees was generally higher during the season than that of the rapidly growing shoots on the heavily pruned trees, although at the end of the season the sap of the two classes was substantially similar in concentration. Thus, both comparisons show that a higher concentration of cell sap is found in slower growing shoots.

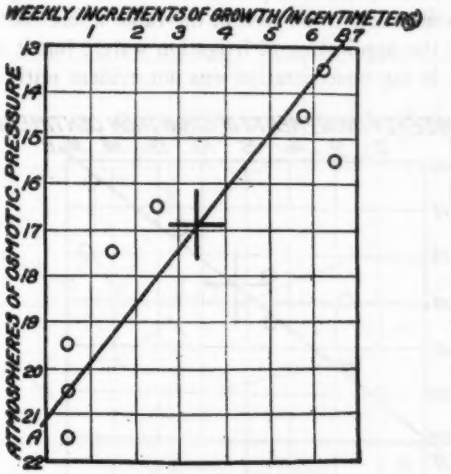


FIG. 3.—Graph showing regression of osmotic pressure on growth increments of unpruned apricot trees (1919).

In order to measure the association between growth and sap concentration I shall employ the correlation coefficient.

The correlation between concentration of cell sap and increment in length is

I..... $r = -0.628 \pm 0.088$ for heavily pruned trees.

II..... $r = -0.823 \pm 0.049$ for unpruned trees.

Reference to figures 3 and 4 shows that regression in the pruned trees is fairly linear, but in the unpruned trees this linearity is doubtful. In the latter case, the significance of the correlation coefficient may be more apparent than real.

It will be readily recognized that factors which contribute to the higher sap concentration of the unpruned trees are associated with the nature of the growth they made. Their slower growth and consequent diminished draft on the plastic materials of the tree should allow a greater

accumulation of soluble materials in their tissues. The smaller water content of the slow-growing wood also contributes to a higher concentration in the sap.

The increased concentration of soluble materials in the sap of both classes of trees as the season advanced is to be referred in part to the foregoing factors and in part to the increase in soluble organic products of photosynthetic activity. With the increase in leaf area and the advance of the season there should be an increase in the content of soluble carbohydrates in the cell sap.

The water content of the soil has an important influence upon sap concentration of the plant (compare Hibbard and Harrington, 7). There are numerous instances to be seen in the table where the sap concentration fell after the application of irrigation water; but it will be noticed that the drop in sap concentration was not evident until, in some cases,

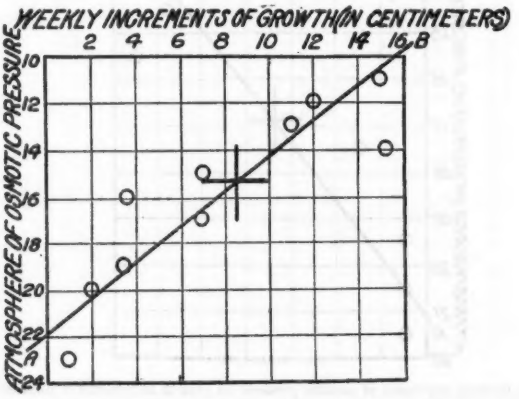


FIG. 4.—Graph showing regression of osmotic pressure on growth increments of pruned apricot trees (1919).

one or two weeks after the application of water. As the season advanced the amount of water in the soil gradually diminished, in spite of the irrigation, and there is little doubt that the gradually diminishing water supply is to some extent causally related to the gradually increasing concentration of the plant sap through the season. It is difficult to express the relationship by a correlation coefficient because the regression between the two pairs of values is not linear. After a certain moisture content (say that of saturation) is reached, a further addition of water would have no effect on the sap concentration of the tree. It may not, however, be entirely improper to attempt to express the relationship as a coefficient of partial correlation. This figure will express the relationship between growth increments and sap concentration, assuming the soil moisture to have been constant. In the case of the heavily pruned trees,

$$r_{ip \cdot w} = -0.525.$$

Taking account of the moisture factor thus reduces the coefficient from -0.628 to -0.525.

SAP CONCENTRATION IN APICAL AND BASAL REGIONS OF APRICOT SHOOTS

Determinations of sap concentration were made at weekly intervals between June 12 and December 4 in the leaves and stems of a 10-cm. zone at both base and apex of apricot shoots. The concentration, as determined by the lowering of the freezing point, is shown graphically in figure 5.

It will be seen that the sap in the apical portion of the stem was more concentrated than that in the basal region. Increases or decreases in the

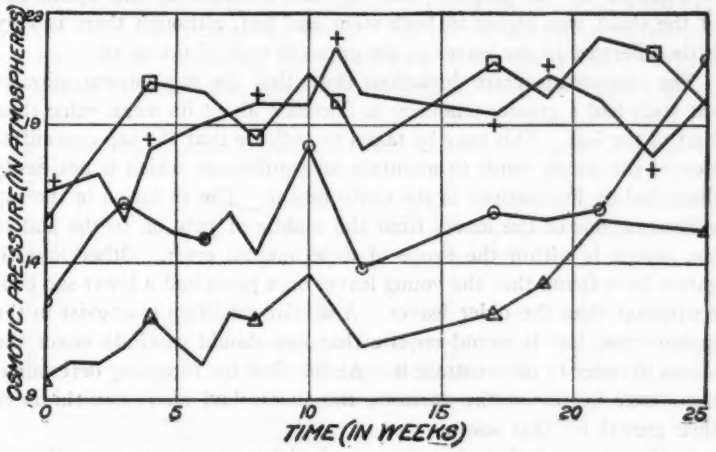


FIG. 5.—Graph showing seasonal variations in sap concentration in apricot shoots.
○=sap concentration of apical 10 cm. of stems.
△=sap concentration of basal 10 cm. of stems.
□=sap concentration of leaves from 10-cm. zone at apex.
+=sap concentration of leaves from 10-cm. zone at base.

one are approximately parallel to increases or decreases in the other. The greater divergence in the last observations is probably due to the dry condition of the samples and to the possibility of error in one or both determinations. In general, the differences between results were sufficiently great to indicate differences well outside the realm of experimental error.

The sap concentrations of the leaves from the different regions show no wide nor consistent differences, though there is a tendency for them to vary in opposite directions—that is, when one rises the other falls, and vice versa. In general, the sap concentration of the leaves was well above that of the stems at corresponding periods, a relation which was pointed out by Heald (*6*).

TABLE IV.—*Mean and root-mean-square deviations of sap concentration in apical and basal regions of apricot shoots*

Part of shoot.	Mean sap concentration.	Root-mean-square deviation.
	Atmospheres.	*Atmospheres.*
Stem, apical	15.83	2.06
Stem, basal	12.59	2.77
Leaves, apical	19.59	1.74
Leaves, basal	18.93	1.68

The mean sap concentrations, shown in Table IV, bear out the facts represented by the graphs. The sap concentration at the apical end of the shoot was higher in both stem and leaf, although there is very little difference in the leaves at the opposite ends of the shoot.

The root-mean-square deviations show that the sap concentration of the stem had a greater tendency to fluctuate about its mean value than that of the leaf. This may be taken to indicate that the sap concentration of the leaves tends to maintain an equilibrium which is not easily disturbed by fluctuations in the environment. The variation in the sap concentrations of the leaves from the middle of July on to the end of the season is within the range of experimental error. Other investigators have found that the young leaves on a plant had a lower sap concentration than the older leaves. A similar condition may exist in the apricot tree, but it would require that one should carefully select the leaves in order to demonstrate it. At the time the foregoing determinations were begun on the apricots, the shoots had made two-thirds of their growth for that season.

It thus appears that there is a gradual increase in concentration of sap from the base to the apex of a growing shoot.

There is, in some quarters, a belief that the apical leaves on young shoots are meagerly supplied with solutes and that the practice of removing the terminal half of the young shoots is justifiable at any time after mid-summer. The determinations made upon these apricot shoots seem to speak against such a belief. From the middle of the summer to the first of December there was little real difference in the sap concentration of the leaves at opposite ends of the new shoots.

The existence of a gradient in the sap concentration of apricot shoots was shown by determinations made on June 10, 1920, using a sample of young shoots having an approximate length of 120 cm. The leaves were removed and the stems were cut into four lengths of 30 cm. each. The sets were designated as A, B, C, and D. A designated the apical set of cuttings and D the basal set.

Sap-concentration determinations were made upon each of these samples separately. The concentrations expressed as atmospheres of osmotic pressure were as follows:

A	13.19
B	11.81
C	10.97
D	10.32

CONCENTRATION OF SAP IN ORANGE SHOOTS AND LEAVES

The leaves of the orange tree persist for more than one year. New shoots commonly arise from axillary buds and may attain considerable length before the subtending leaf falls. Determinations were made of the sap concentration in new shoots of the Washington Navel orange and of the old leaves subtending them. The leaves had grown to maturity in the summer preceding the appearance of the shoots and might be supposed to have some physiological relation to their axillary shoots.

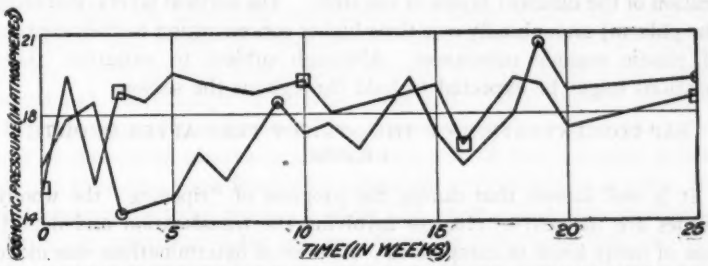


FIG. 6.—Graph showing seasonal changes in sap concentration in orange shoots and their subtending leaves.
○=sap concentration of young shoots.
□=sap concentration of the subtending leaves.

There was, however, no general relationship indicated by the sap concentration of the two members. Figure 6 represents graphically the changes in sap concentration of leaves and their axillary shoots from April 15 to October 9. During the first few weeks the sap concentration of the stem appeared to fluctuate and reached the low point for the season about May 1. From May until October there was a general tendency for the sap concentration to rise, though not to so marked a degree as was seen in the apricot. Throughout most of the summer the concentration of the leaf sap was greater than that of the shoot sap. The mean of the determinations of the leaf sap was 18.4 atmospheres and of the shoot sap 17.3 atmospheres.

The root-mean-square deviation of a series of values from their mean, as stated above, is an excellent measure of their dispersion. In this case the root-mean-square deviation of the leaf-sap concentration is 1.21 atmospheres and that of the shoot sap is 1.64 atmospheres. This shows that the concentration of sap in the leaves was subject to slightly less

fluctuation during the period of the observations than that of the shoots. In all cases these leaves were not more than 1 year old and were performing the functions common to orange leaves of their age. It seems difficult to escape the conclusion that in some way the concentration of solutes in the leaves tends to reach and maintain an equilibrium, and that this equilibration occurs regardless of the variations in concentration which simultaneously take place in the adjacent shoots.

CONCENTRATION OF THE SAP IN VARIOUS LAYERS OF THE APRICOT SHOOTS

The following osmotic pressures were found in a sample collected on June 27: mature leaves, 17.12 atmospheres; cortical layers of the stem, 13.82 atmospheres; woody, subcortical layers, 10.21 atmospheres. These figures indicate that the sap of the wood is less concentrated than that of the leaves and are in entire agreement with those previously obtained. They show quite remarkable differences in the sap concentration of the different layers of the stem. The cortical layers (including the phloem) undoubtedly owe their higher concentration to their content of plastic organic substances. Although subject to variation, these relations might be expected to hold throughout the season.

SAP CONCENTRATION OF THE APRICOT TREE AFTER GROWTH CEASES

It is well known that during the progress of "ripening" the woody tissues are the seat of changes involving the translocation and deposition of many kinds of compounds. A series of determinations was made after the shoots on these trees ceased to show further elongation to see whether there were appreciable changes in sap concentration in the early part of the dormant period.

TABLE V.—*Sap concentration of apircot shoots during fall and early winter*

Date.	Osmotic pressure.	
	Unpruned trees.	Heavily pruned trees.
	Atmospheres.	*Atmospheres.*
Oct. 23	18.60	15.81
Nov. 6	19.10	17.90
20	19.00	17.20
Dec. 4	16.33	17.22
18	19.10	22.30
Jan. 29	15.85	18.75

These figures show that there are appreciable changes in the concentration of the sap even though no active growth is taking place. The changes may, however, be referred in part to changes in the amount of

soil moisture present. During November and December there were light rains which did not penetrate deeply into the soil and did not affect the concentration of the cell sap of the trees. On January 4, 0.585 inches of rain fell, and on the three succeeding days 5.2 acre-inches of irrigation water were applied. The effect of this increased supply of soil moisture is seen in the lower concentration of sap in the samples taken on January 29. The effect of the increased amount of water intake was to dilute the sap of the tree, even though active growth had ceased.

SAP CONCENTRATION AND FRUITFULNESS

The observations made upon these fruit trees may throw some additional light upon the relationships between vegetative and fruiting activity of the tree. It appears that lower sap concentration is associated with abundant water intake and rapid growth. Severe pruning, which also stimulated active vegetative growth, caused *pari passu*, a lowering of the concentration of sap in the tree.

Horticulturists have long recognized that those conditions which are associated with lower sap concentration are opposed to fruit bearing in a tree. With the data now in hand it seems possible to point out some additional relationships of interest. The most rapid growth occurs in the early part of the season. The apricot shoots in 1919 made about half of their total growth in the first one-fifth of their growing period. By the time that three-fourths of the length growth had been made, the sap concentration had reached a fairly high value, which was maintained during the remainder of the season. Now it is well known that this time of higher sap concentration is the time during which the fruit buds for the following year are developing on the tree. The various lines of evidence lead to the conclusion that higher sap concentration is associated with slower growth and fruit-bud formation. At the present time, however, it seems impossible to say which one of the conditions is cause and which is effect. Differences in the sap concentration of the stem at the apical and the basal ends of the shoots are so well marked as to be unmistakable, yet it is somewhat difficult to orient one's views to fit the facts. The sap concentration of entire shoots, including stems and leaves, was lower during periods of rapid growth and higher during periods of slower growth. Yet, when we note that the sap concentration of the rapidly growing apical region of the shoot was uniformly higher than that of the slowly growing basal region, the condition seems paradoxical. The condition seems the more paradoxical when one remembers that the apical portion of the stem has a higher water content and that the content of solutes must, therefore, be correspondingly higher in order to show a higher concentration in the expressed sap.

We should remind ourselves, however, that growth is not wholly regulated by concentration *per se*. The composition of the sap, no less than

its total concentration, affects the activity of the cell. Attention has recently been called to the effect on plant growth of inhibiting substances resembling chalones (*9*, *14*). The absence of these growth-inhibiting substances in the apical portion of the shoot accounts in large measure for the more rapid growth of that region. There are also numerous lines of evidence which indicate that the sap of the apical region of the stem promotes vegetative growth because of its greater content of nitrogenous substances, while the slowly growing basal portion of the shoot is favorable to fruit-bud formation because of its greater content of carbohydrates (*8*). It goes without saying that we must recognize qualitative as well as quantitative differences in the plant sap in analyzing its

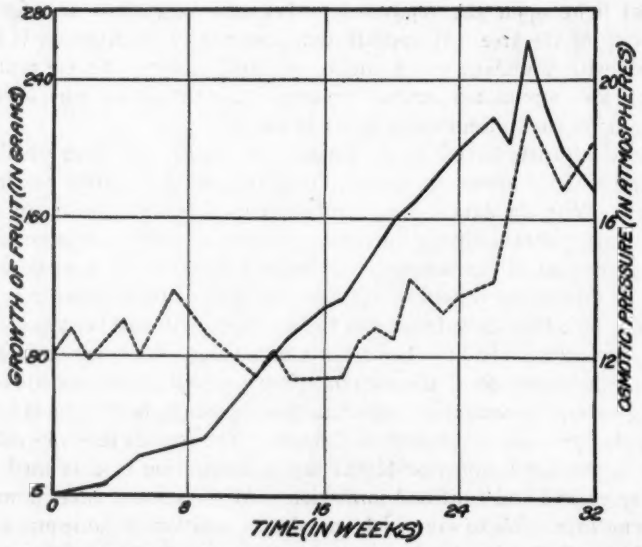


FIG. 7.—Graph showing growth and sap concentration of Golden Nugget navel oranges. Average weight of fruits is shown by solid lines, sap concentration of fruits by broken line.

effects on growth. The evidence, however, indicates that an increasing sap concentration in the shoot as a whole retards vegetative growth, while a decrease in the sap concentration of the whole shoot favors growth.

SAP CONCENTRATION AND THE GROWTH OF ORANGE FRUITS

The orange fruit was selected for study because it has a relatively long period of growth and develops on a tree which continuously bears green foliage. The variety employed is a strain of the navel orange known as "Golden Nugget." Determinations began on June 5, 1918, and were continued at weekly intervals until January 16, 1919. The mean weight of fruits on the former date was 0.39 gm. The growth rate was rather slow from the beginning of the observations until the end of the ninth

week; then a period of more rapid growth set in, which lasted until the twenty-sixth week (Dec. 1). Toward the close of the period there was considerable fluctuation in the weight of fruits, largely because of errors in sampling, but the final mean weight was somewhat over 200 gm. The courses of the growth process and of the sap concentration of the fruit are shown in figure 7. During the first nine weeks, while the fruits were growing slowly, their sap concentration varied between 12 and 14 atmospheres of osmotic pressure. When more rapid growth began, the sap concentration dropped to a pressure between 11 and 12 atmospheres, but subsequently gradually rose. As the fruit approached maturity there was a great increase in its sugar content and a consequent increase in the concentration of the sap.

During the first half of the growth period it is quite evident that rapid growth is accompanied by a lower sap concentration. In the latter half of the growth period it is more difficult to ascertain the relationships between sap concentration and growth because of the fact that while the fruit is still growing it begins to accumulate increasing amounts of soluble carbohydrate.

SUMMARY

(1) Observations on the growth and sap concentration of young trees showed that the two variables have a tendency to vary in opposite directions—that is to say, rapid growth is associated with a generally lower concentration of sap in that shoot, while slower growth is accompanied by higher concentrations of sap.

(2) There was a gradual increase in sap concentration as the season advanced. In apricot trees the concentration continued to increase for some time after active growth had ceased. The accumulations of solutes in the plant sap is unquestionably related to the synthetic metabolism of the tree as the season advanced, though there is some evidence that diminished water absorption was partially responsible for the increased sap concentration.

(3) Of several environmental factors measured, soil moisture was the only one having an obvious effect upon sap concentration. The addition of water to the soil usually diminished the concentration of the plant sap.

(4) The sap concentration of shoots on trees heavily pruned was lower than that of shoots on trees not pruned, because of the more rapid growth of the former.

(5) A concentration gradient appears to exist in the shoot. The concentration of the sap in the apical portion of a stem was greater than that in the basal region. The sap concentration in the stems showed a greater tendency to fluctuate than that in the leaves.

(6) Lower concentrations of plant sap in the shoot as a whole appear to be associated with abundant water intake and rapid vegetative growth.

Higher concentrations are associated with slow growth and fruit-bud formation.

(7) The results seem to indicate that the practice of summer pruning fruit trees is not only unnecessary but may be detrimental.

(8) Observations upon the growth and sap concentration of shoots and fruits of the orange tree confirm those made on the apricot tree.

LITERATURE CITED

(1) CHANDLER, W. H.
1914. SAP STUDIES WITH HORTICULTURAL PLANTS. Mo. Agr. Exp. Sta. Research Bul. 14, p. 489–552, illus. Bibliography, p. 535–539.

(2) DIXON, H. H.
1914. TRANSPIRATION AND THE ASCENT OF SAP IN PLANTS. viii, 216 p., illus. London. "Literature" at ends of chapters.

(3) ——— and ATKINS, W. R. G.
1912. VARIATIONS IN THE OSMOTIC PRESSURE OF THE SAP OF ILEX AQUIFOLIUM. *In* Sci. Proc. Roy. Dublin Soc. n. s. v. 13, p. 220–238.

(4) HARRIS, J. A., and GORTNER, R. A.
1914. NOTES ON THE CALCULATION OF THE OSMOTIC PRESSURE OF EXPRESSED VEGETABLE SAPS . . . *In* Amer. Jour. Bot., v. 1, p. 75–78.

(5) LAWRENCE, John V., and GORTNER, Ross Aiken.
1916. THE CRYSCOPIC CONSTANTS OF EXPRESSED VEGETABLE SAPS, AS RELATED TO LOCAL ENVIRONMENTAL CONDITIONS IN THE ARIZONA DESERTS. *In* Physiol. Researches, v. 2, no. 1, p. 1–49. Literature cited, p. 49.

(6) HEALD, Fred. D.
1902. THE ELECTRICAL CONDUCTIVITY OF PLANT JUICES. *In* Bot. Gaz., v. 34, no. 2, p. 81–92, 2 fig.

(7) HIBBARD, R. P., and HARRINGTON, O. E.
1916. DEPRESSION OF THE FREEZING-POINT IN TRITURATED PLANT TISSUES AND THE MAGNITUDE OF THIS DEPRESSION AS RELATED TO SOIL MOISTURE. *In* Physiol. Res., v. 1, p. 441–454.

(8) KRAUS, E. J., and KRAYBILL, H. R.
1918. VEGETATION AND REPRODUCTION WITH SPECIAL REFERENCE TO THE TOMATO. Oregon Agr. Exp. Sta. Bul. 149, 90 p., illus., pl. Literature cited, p. 87–90.

(9) LOEB, Jacques.
1917. THE CHEMICAL BASIS OF AXIAL POLARITY IN REGENERATION. *In* Science, n. s. v. 46, no. 1197, p. 547–551.

(10) LUTMAN, B. F.
1919. OSMOTIC PRESSURES IN THE POTATO PLANT AT VARIOUS STAGES OF GROWTH. *In* Amer. Jour. Bot., v. 6, p. 181–202. Literature cited, p. 202.

(11) REED, H. S.
1920. THE DYNAMICS OF A FLUCTUATING GROWTH RATE. *In* Proc. Nat. Acad. Sci., v. 6, no. 7, p. 397–410, 3 fig.

(12) ———
1920. THE NATURE OF THE GROWTH RATE. *In* Jour. Gen. Physiol., v. 2, p. 545–561. Bibliography, p. 561.

(13) ———
1920. SLOW AND RAPID GROWTH. *In* Amer. Jour. Bot., v. 7, no. 8, p. 327–332. Literature cited, p. 332.

(14) ——— and HALMA, F. F.
1919. THE EVIDENCE FOR A GROWTH-INHIBITING SUBSTANCE IN THE PEAR TREE. *In* Plant World, v. 22, p. 239–247.